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The effects of FMD-induced mass livestock slaughter on greater horseshoe bats in the Forest of Dean

R D Ransome
School of Biological Sciences
University of Bristol
Woodland Road
Bristol BS8 1UG

and

D J Priddis
Nordown
Ring Fence
Woolaston Common
Nr Lydney
GL15 6NX

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Summary

The objectives of this study were to:

1. investigate the effect of the removal of grazing livestock from the Forest of Dean by slaughter to prevent the spread of foot and mouth disease in spring 2001 on the summer and winter diet of greater horseshoe bats occupying the maternity roost at Dean Hall and hibernating in the Forest of Dean, in comparison with those at Woodchester Mansion, where no slaughter took place;

2. investigate the effect of the slaughter on population parameters from the two maternity sites, one within the region affected by slaughter; the other outside;

3. investigate the effect of the slaughter on the growth of juvenile bats born at the two maternity sites;

4. to make recommendations for measures within the FMD affected regions to maintain favourable levels of insect dung fauna to sustain bat populations over the long term.

The slaughter of grazers due to FMD, in the spring of 2001, had little impact upon the consumption of insect prey by bats at the Dean Hall and Woodchester roosts from late April to mid July in the summers of 2001 and 2002. Hence the whole of pregnancy and early to mid lactation was largely unaffected by FMD.

FMD slaughter had serious impacts upon the consumption of the small dung beetle (*Aphodius*), by both adult and young bats, from late July to October in the summers of 2001 and 2002 at both roosts. Alternative, secondary prey were eaten, but these failed to provide the quantity and/or nutritional quality necessary to adequately sustain females late in their lactation period.

During the late lactation period in three different summers (1997, 2001 and 2002) bats at Woodchester showed an 11.5% fall in consumption per bat through these years, and no change in juvenile mortality at this roost was noted post FMD. At Dean Hall consumption levels fell by 31.5% through the same period. Body condition of juveniles fell significantly after FMD at both roosts, compared with previous summers. More juveniles died within the Dean Hall roost than pre FMD.

Even though the roost was outside the slaughter area, the survival rates of juvenile cohorts born at Woodchester fell after FMD. Presumably survival rates were even lower at Dean Hall, but no data were available.

Winter diets were investigated at both roosts, and two major hibernation sites within the Forest of Dean. The diet quality at Dean Hall after FMD was superior to that at Woodchester, especially in 2002/3, with about 50% being from the large dung beetle (*Geotrupes*) being eaten, compared with very low levels at Woodchester. Neither the amounts of prey consumed by individual bats at Cinderford and Symonds Yat, nor their diet content showed any deterioration over the two winters after FMD slaughter. *Geotrupes* consumption remained very high (over 90%) at both sites.

Although the winter diet of bats within the Forest of Dean remained of higher quality than at Woodchester and near Nailsworth, the numbers of bats at Cinderford fell markedly in the winter of 2002/3 by nearly 50% compared with two winters earlier. For the first time, bats born at Dean Hall in 2002 were caught in several distant hibernacula near Nailsworth the following winter.

To mitigate against the damage caused by FMD slaughter, we recommend that the environmental prescriptions made by Ransome (1996, 1997a) continue to be vigorously implemented, since this study reinforces their value. It is especially important for significant numbers of cattle to be grazed as close to roosts as possible from mid July until at least late August, and preferably to mid October.

Habitat structure for foraging bats should be of the highest quality within the young sustenance zone, up to 1 km from each roost. This measure will ensure that *Aphodius* beetles will be concentrated just outside roosts, when juveniles first start to forage, since many are drawn from much larger populations further away.

In order to sustain large populations of *Aphodius* and *Geotrupes* beetles in the surrounding areas, land managers should be encouraged, by appropriate support measures, to maintain grazers at distances up to at least 10km from the roost. As this distance will normally encompass both the maternity roost and important hibernacula, the grazers may be cattle, sheep, horses or deer, and they should be kept at sustainable densities that allow them to be kept on pastures throughout the year.

Cattle grazing in mid to late summer, followed by sheep or horses in winter is a good combination. Sheep grazing adjacent to woodland in winter is especially recommended, as sheep maintain a short sward that favours cockchafers and tipulids. Habitat structure should also be high quality at distances between 1km and 3 km from the maternity roost, and around important hibernacula.

Habitat structure should also be of high quality very close to important hibernacula, where bats are most likely to need to forage in winter. Cattle and/or sheep and/or horses should be grazed within 1km, and preferable within 0.5km, of their entrances from early September through to the following April. If horses are grazed over-winter, their dung should be left in situ, and not collected.

Contents

Introduction

The outbreak of foot and mouth disease (FMD) in February 2001 lead to the slaughter of over 4.23 million cattle, sheep, pigs, goats, deer and other potential carriers in the UK (Defra website, March 2003 data). Some 44% of the confirmed outbreaks were in Cumbria. Of the 4.23 million animals slaughtered, 82.6% were sheep, and 13.8% were cattle. The impact of the loss of dung as a result of the removal of these grazers upon wildlife has not previously been assessed. Herbivore dung supports a large range of invertebrate animals, including adult insects and their larvae that are important in the diets of many birds and mammals.

Dietary research (Ransome 1996, 1997a, 2000) has shown that the dung beetle *Aphodius rufipes* is an important component of the summer diet of greater horseshoe bats. In exposed conditions it prefers the dung of cattle, but will also use horse, sheep and deer dung, especially in shady habitats (Landin 1961). Although these beetles are eaten by adult bats, they are a critical dietary item for young bats when they first begin to forage. The 1 km zone around maternity sites has been identified as a crucial foraging area in which young bats develop their foraging skills and recommendations have been put forward for ways of enhancing bat populations through appropriate land-management practices to increase the availability of *Aphodius* in this area.

Dietary research of these bats in winter (Ransome 2002) has shown that large dung beetles, *Geotrupes spp.*, provide a major dietary component of these bats in the Forest of Dean, and to a lesser extent to other populations around Bristol. Different species of this genus fly during most winter months. Most are favoured by cattle dung, but horse and sheep dung within park-land and forests are also valuable. Winter foraging is important to avoid starvation by certain age and sex groups, especially adult male and first-year bats of both sexes (Ransome 1968).

The greater horseshoe bat is an endangered species that is restricted to the south-western parts of England and Wales. About 15% of the FMD confirmed cases occurred within its range, including a major outbreak within the Forest of Dean. This area is a candidate Special Area of Conservation, primarily because of its importance to horseshoe bats.

Populations of these bats fell at all known maternity roosts during the summers of 1986 and 1987, due to the accumulative impact of severe climate over the previous five years (Ransome 1989). Since then there has been a slow recovery at most roosts, almost to the levels of the early 1980's, by 2000.

The maternity colony of greater horseshoe bats at Dean Hall, near Cinderford in the Forest of Dean, enjoyed a favourable population status prior to FMD outbreak relative to others nearby (Ransome 1998). This was believed to be due to the high quality of its surrounding habitat and foraging opportunities all year round.

There are therefore sound empirical reasons to believe that the slaughter to contain the FMD outbreak will have had important impacts upon the diet of these bats, and indirectly upon the growth and survival of their young. Possibly the survival of certain older sex and age groups may also have been adversely affected.

In the areas around the greater horseshoe bat maternity roosts at Dean Hall in the Forest of Dean, and near to Braunton Burrows, Devon, a high proportion of the livestock was slaughtered during the outbreak of foot and mouth disease (FMD) starting in February 2001.

Within a 10mile (16km) radius of Dean Hall, nearly 46,000 sheep and 13,000 cattle were slaughtered due either to being on confirmed FMD premises (IPs), or those in dangerous contact within contiguous areas to infected premises (DC contiguous premises). These figures do not include animals that were dangerous contacts within non-contiguous areas (DC non contiguous premises), and those slaughtered on suspicion. The total numbers slaughtered are likely to be more than double these totals. Hence at least 118,000 animals were lost to the grazing ecosystem within this range.

The consequence of the slaughter must have been a significant reduction in the availability of animal dung in 2001, and possibly in subsequent years in the absence of re-stocking of grazers to former levels. However, both *Aphodius* and *Geotrupes* beetles have year-long life cycles. Their larvae feed on fresh dung in one year, and emerge as adults in the following year, when fresh dung attracts concentrations of flying adults to grazed pastures where bats can catch them. This means that the impact of the slaughter upon bats may not have become apparent for at least a year afterwards, and any restocking that subsequently occurred may have helped to reduced its effects.

This project investigates the impact on the bats of the removal of a significant proportion of the domestic livestock within the Forest of Dean. Initially it was hoped to include data from a maternity site near Braunton Burrows. Some donated summer samples of droppings were collected for dietary analysis from the roost. However, as these were only available for a limited period in mid summer, at a time when bats do not feed on dung beetles, and no historical data were available for this site, it was excluded from the investigation.

1. Overview of the scientific plan used in the study

1.1 Introduction

The scientific plan was designed to answer the following questions:

1. Did the consumption of dung-dependent insects fall significantly in the summers of 2001 and 2002 at the Dean Hall maternity site that was affected by the slaughter?

2. Did the consumption of dung-dependent insects fall significantly in the summers of 2001 and 2002 at the Woodchester Mansion maternity site that was not directly affected by the slaughter?

3. Did the consumption of dung-dependent insects fall in the following two winters at these maternity roosts, and major wintering sites?

4. If significant dietary changes were detected, were they linked to changes in the growth of juvenile bats at the two maternity sites?

5. Were the populations of bats at the two summer roosts affected by the slaughter?

1.2 Methods

The broad strategy of the study was as follows. First we characterised the diets at the two maternity roosts for several summers before the FMD outbreak, to establish the normal variation occurring. Then we analysed the diets at the two roosts for the two summers and winters following the slaughter to look for differences that were associated with the loss of dung. The Woodchester colony, being outside the FMD slaughter area, was believed to provide a control situation for any changes that were noted at the Dean Hall colony.

This investigation was possible since a series of dietary studies had already been undertaken at Woodchester and Dean Hall colonies in some of the years before the FMD slaughter. In other years dropping samples had been collected and stored, but not analysed until the present study.

We used the methods described in Ransome (1996), to discover the diet by analysing samples of bat droppings from summer collections made in previous years at Dean Hall (1995 to 1998). Data were used to characterise the diet on a weekly basis. Paired weekly samples from Dean Hall and Woodchester Mansion were statistically compared for these summers, with the exception of 1995. In 1995 data were not collected on a weekly basis, and so could not be compared. Data from the summers of 2001 and 2002 were used to compare diets at the two sites, with data from previous years.

As well as characterising the diets of these bats in the pre and post FMD slaughter phases, the dry mass of weekly dropping collections at the two roosts were used to estimate the amount of food consumed. This was only possible for one summer before FMD and the two summers afterwards.

Statistical comparisons were made using Minitab version 13. All diet percentage data were arcsine transformed in an attempt to normalise them (Whitaker 1988). Unfortunately this was not successful. Because of this, non-parametric statistics (Mann-Whitney tests) were usually used to assess the significance of differences between paired sets of diet data.

Winter samples were donated from important underground sites in the Forest of Dean. They were Buckshaft in early December 2001 and 2002, and Symonds Yat in February 2002 and 2003. Data were compared with those from pre FMD winters as published by Ransome (2002).

Two other kinds of studies were concurrently carried out alongside dropping collections. They were exit counts of adult bats flying out to forage at dusk from each roost, and growth studies of the young that were left behind in the roost by their mothers. The data generated by these studies at Dean Hall (by DJP and assistants) and Woodchester Mansion (by RDR and assistants) were compared, particularly with respect to the number of births, birth timing, body condition and growth of the young, together with the pattern of roost occupation by each colony. Comparisons were made between the two sites and with previous years.

2. Summer diets of bats at Dean Hall and Woodchester Mansion before the slaughter

2.1 Introduction

Ransome (1996 and 1997a) developed the following working hypothesis to explain dietary changes of greater horseshoe bats throughout each summer following studies at eight widely dispersed maternity roosts. It has been updated in the light of further studies.

Greater horseshoe bats are normally highly selective foragers. Individual bats normally select a single prey item at each foraging bout. This may be key prey, such as moths, or secondary prey, such as tipulids. Mothers and young feed on their respective key prey items if they are abundant (mothers on moths; young on Aphodius beetles in mid to late summer). If the item selected is absent, or in short supply, mixtures of key prey and/or secondary prey are consumed. Mixtures of four, or more, prey items indicate severe dietary stress.

2.2 Dietary changes through the summer

(a) The preferred key prey in April for all bats that have survived the previous winter is the large dung beetle *Geotrupes*.

(b) In May, the preferred key prey is the cockchafer *Melolontha melolontha.*

(c) In April and May, in the absence of sufficient key prey, bats switch to secondary prey such as tipulids, caddis flies and the ichneumonid *Ophion*. As a last resort they eat small dipterans.

(d) In June and early July, pregnant females feed on moths, their key prey at that time, and continue to do so after giving birth, until late August. They usually avoid *Aphodius rufipes* even when they are abundant, as long as moths are in good supply. If both are in poor supply they switch to summer chafers (*Amphimallon* or *Serica*).

(e) Moth supplies usually fall steadily in August and September, due to phenological population declines, or rapidly at a particular dawn or dusk due to temporary low temperatures. If either happens adult bats switch to secondary, single prey items, or combine moths with them. Tipulids are often the first alternative, but *Aphodius rufipes* is also taken. In very cold spells ichneumonids, of the *Ophion luteus* complex are consumed. They are common prey in October and through the winter (Ransome 2002) as they can fly at low ambient temperatures. However in summer they are used as a last resort.

(f) Juvenile bats do not feed at all until they are about 29 or 30 days old, when they normally feed on *Aphodius rufipes*, which is their key prey. This dung beetle species is a fairly small (90mg), easily-caught and usually abundant prey, which reaches peak numbers at the time that the young normally start to feed in early August. However, if drought delays its flight activity, or low temperatures prevent flight at a particular feed, they either switch to secondary prey, or abandon feeding, rather than combine more than two prey types at a single feed. Alternative (secondary) prey are usually tipulids, small dipterans or ichneumonids until the age of 42 days. After this age moths may also be caught probably because the young can Doppler shift compensate at about this time (Konstantinov 1989), allowing them to catch faster-flying prey.

2.3 Diets at Woodchester Mansion and Dean Hall maternity roosts

This section examines the diets of bats at the two roosts for several summers before the slaughter, in order to characterise them.

Diets of insectivorous bats are normally determined by analysis of faecal pellets (droppings), or from culled remains left at feeding posts (Jones 1990), since direct observation of prey capture at night is not feasible, nor is stomach analysis (Whitaker 1988). Faecal pellets contain mostly exoskeletal protein and chitin, both very resistant substances. Skeletal fragments in faeces permit recognition of prey to at least order level, and often to families, species groups and even single species in some cases.

Bats eat large amounts of insect food very quickly, digest it rapidly, and egest the bulk of the remains in a few hours. Greater horseshoe bats egest 70% of a full stomach within eight hours of feeding (Ransome 1978), most of it within roosts from where samples may be collected.

2.4 Methods

2.4.1 Period of faeces collection beneath maternity clusters

Weekly samples of bat droppings were collected from the maternity roosts at Dean Hall and Woodchester over the summers of 1995 to 1998 to provide the pre-slaughter samples. Droppings accumulated on heavy-gauge polythene sheets spread beneath each colony that were swept clean after collection to avoid contamination. The sampling protocol described by Ransome (1996), was followed from 1996. In each summer 11 weekly samples were collected, starting with the last week of April and ending with the first week of October. Samples were collected as follows:

1. Last week of April; first week of May (early pregnancy for breeding females).

   These are weeks 1 and 2 of the study.

2. Last week of May; first week of June (mid pregnancy).

   These are weeks 3 and 4 of the study.

3. Last week of June; first week of July (late pregnancy/early lactation)

   These are weeks 5 and 6 of the study.

4. Last week of July; first week of August (mid to late lactation/ early juvenile flights)

   These are weeks 7 and 8 of the study.

5. Last week of August; first week of September (weaning/juvenile independence)

   These are weeks 9 and 10 of the study.

6. The week starting at the end of September, that ended in early October (independent juveniles)

   This is week 11 of the study.

2.4.2 Faecal analysis

The methods used to discover the diet from bat faecal pellets (droppings) are fully described by Ransome (1996; pages 5 and 6). The only difference was in the number of pellets analysed per weekly sample. Instead of 16 per week, the number was reduced to 12 per week, as this reduction did not affect the reliability of the data.

2.5 Results

2.5.1 Dietary content by year, site and season compared

Data from the four summers for the complete sampling period are summarised separately for the two maternity colonies in figures 1 and 2.

The data are remarkably similar overall for the two sites. Moths were the major key prey item closely followed by *Aphodius* beetles. Differences, as shown by Ransome (1997a), mainly relate to the secondary prey. At Dean Hall they were mainly tipulids, whereas at Woodchester a range of prey were eaten. However, as *Aphodius* beetles are only eaten from weeks 7 to 11 of the sampling period, it was more important to compare the diets at the two roosts annually over this more limited period. Figures 3 to 5 illustrate data for the years before FMD when weekly samples were obtained. This did not include 1995 as data were not collected on a weekly basis at that time.

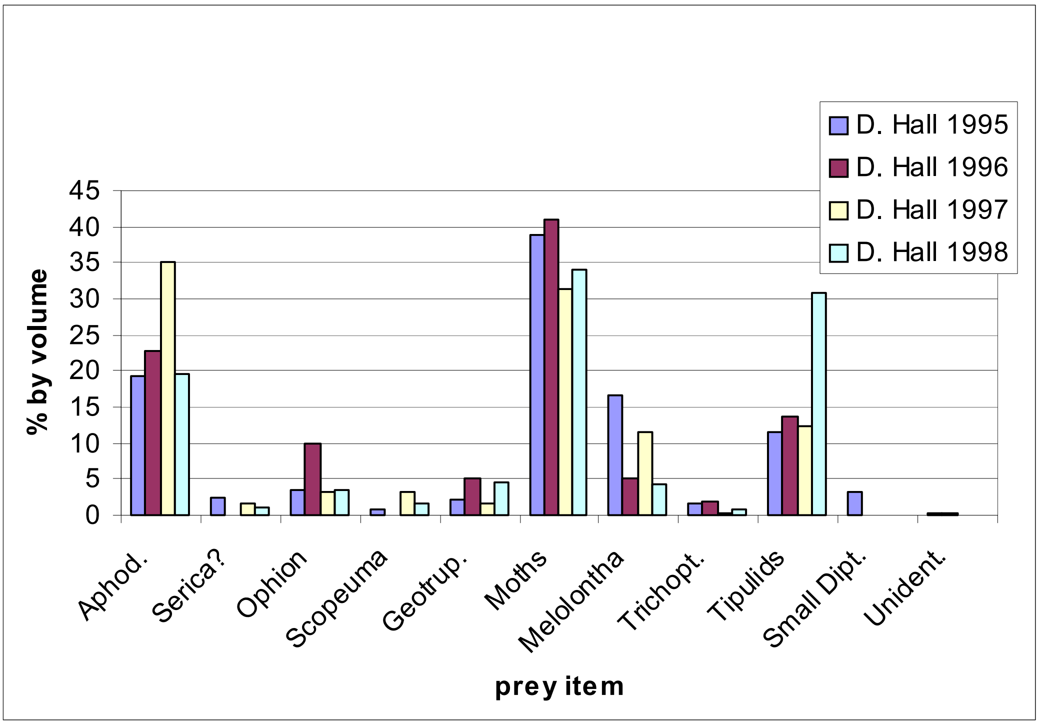

Figure 1 Summer diet at Dean Hall prior to the foot and mouth slaughter

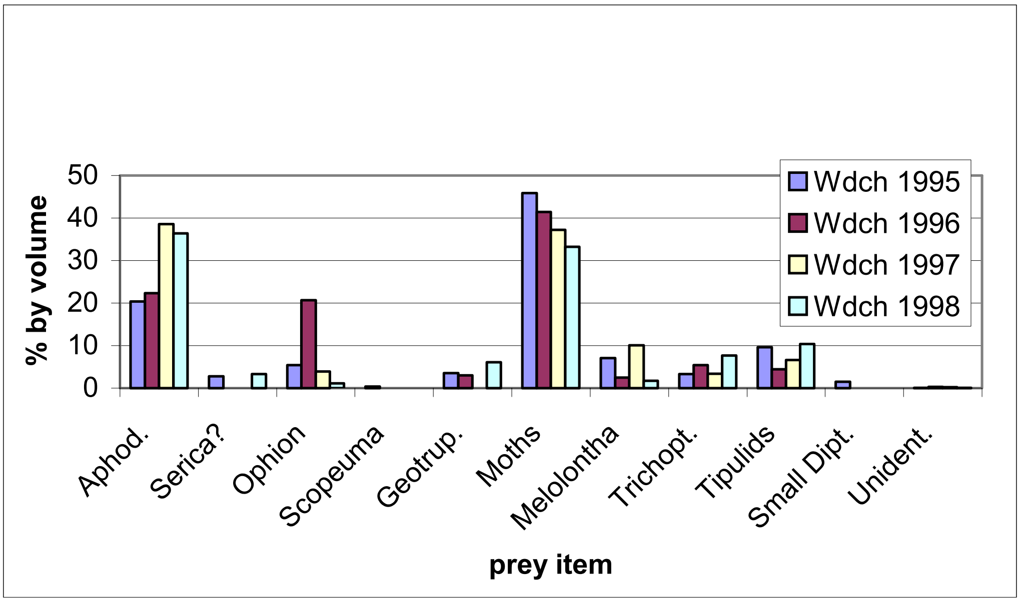

Figure 2 Summer diet at Woodchester prior to the foot & mouth slaughter

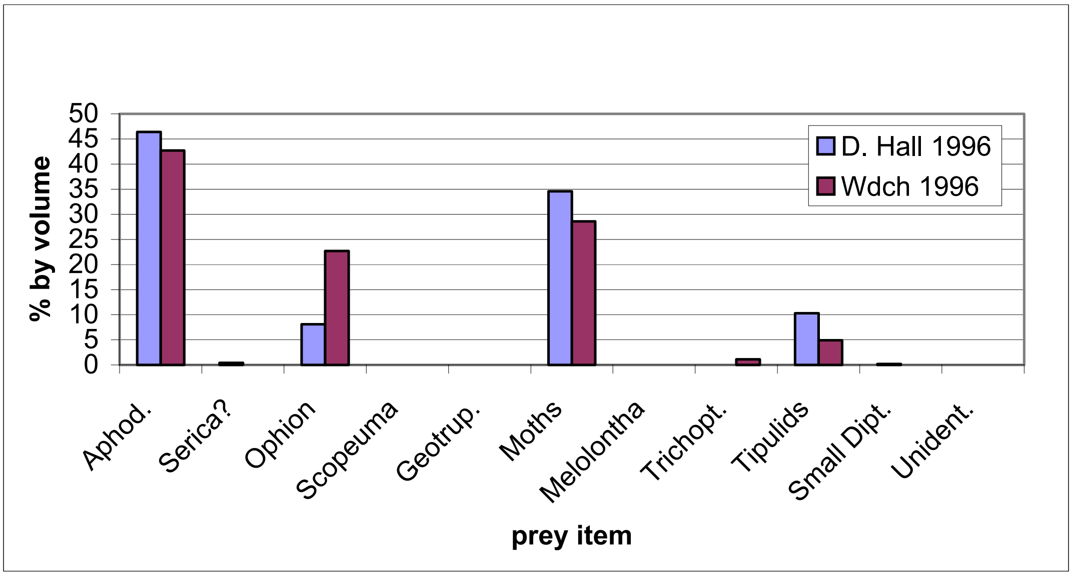

Figure 3 Summer diet totals for weeks 7 to 11 at the two roosts in 1996

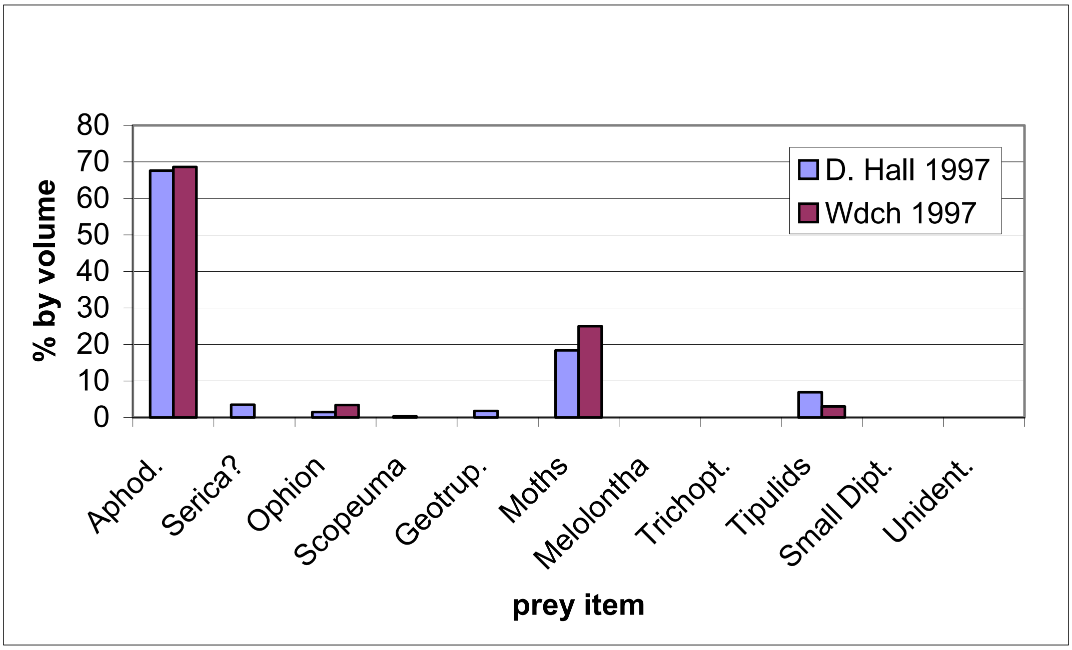

Figure 4 Summer diet totals for weeks 7 to 11 at the two roosts in 1997

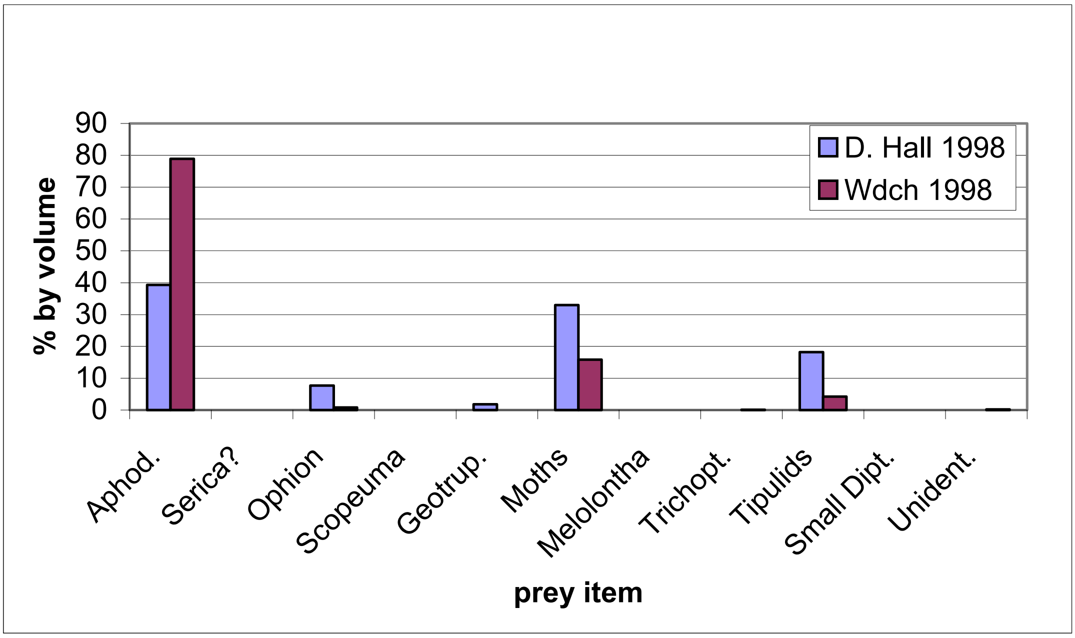

Figure 5 Summer diet totals for weeks 7 to 11 at the two roosts in 1998

Figures 3 and 4, for the summers of 1996 and 1997, show remarkable similarity between the diets at the two maternity roosts for weeks 7 to 11. This is particularly true of the *Aphodius* and moth consumption. *Ophion* consumption was higher at both sites in the cool summer of 1996, but greatest at Woodchester. In the warm summer of 1997, consumption of *Ophion* was very low at both roosts.

Figure 5, for summer 1998, shows the greatest diet differences between the two sites during the pre-FMD period. Dean Hall bats ate significantly fewer *Aphodius* and more moths than Woodchester bats. Table 1 summarises the significant differences between prey consumption at the two roosts using Mann-Whitney statistical calculations on the arcsine-transformed data for these years.

Table 1 Significant prey consumption differences between Dean Hall and Woodchester bats pre FMD for weeks 7 to 11 (Mann-Whitney tests)

Roost	Year	Variable	Sample size	Median	W	P (adj)
Woodchester	1998	Aphodius	60	77.1	4612.5	**0.000**
Dean Hall	1998	Aphodius	60	38.1	"	"
Woodchester	1998	Moths	60	0.00	3159.5	**0.0076**
Dean Hall	1998	Moths	60	24.70	"	"

NB When arcsine transformed, 100% = 90; 50% = 45, and 0% = 0. P values for both analyses are in bold to show that they are significant. There were no significant prey consumption differences between the two roosts in years 1996 & 1997 during weeks 7 to 11.

2.6 Discussion

Data from collections of faecal pellets produced by clusters of bats over time poses some inherent problems of interpretation. The individual bats present in the cluster may change, and even if they remain the same, their reproductive state is constantly changing and the level of their contribution to the sample collected alters. Ransome (1997b) showed that the amounts of food consumed before dawn, as judged by dry mass of droppings produced, varies markedly with reproductive state during the summer. Also, young bats do not feed when they first leave the roost, but show a rapid rise in amounts consumed between 29 and 55 days of age during late July and August (Jones and others 1995). Later on in September, most mothers leave the roost, so that only juveniles remain in early October at Woodchester. Adult bats have only been caught once at Dean Hall, so the pattern of occupation is not known. However, the total numbers counted out indicate that many adults must remain with the juveniles well into October. This situation does not occur at Woodchester.

Despite these potential problems, the summary data illustrated for the four summers of complete samples (Figures 1 & 2) show considerable similarities between the diets at the two colonies. This shows the conservative nature of the diets of these bats, since the four summers sampled showed considerable extremes of climate, and birth timing. Summer 1995 was hot and dry, with a drought that continued until late August. Summer 1996 was wet and cold early on, and led to late births that summer, as predicted by Ransome and McOwat (1994). In contrast, summer 1997 had a very warm spring and summer that led to very early births and successful survival of the young born at Woodchester in 1996 and 1997.

Overall the diets were remarkably similar, including the period from weeks 7 to 11, when *Aphodius* beetles were eaten (Figures 3 to 5). In 1998 Woodchester bats ate much higher levels of these beetles than the Dean Hall bats. The latter ate more moths and tipulids instead, though differences in tipulids consumption were not significant. Moths and tipulids are eaten by adults, rather than juveniles, and these differences may reflect the higher availability of these prey compared with *Aphodius* in the Forest of Dean, and/or the higher number of adult bats in the colony. At Woodchester, special grazing agreements were in place to promote dung insect fauna from the mid 1990s, so *Aphodius* may have been the more abundant prey there in 1998.

3. Summer diet of bats at Dean Hall and Woodchester Mansion after the slaughter

3.1 Introduction

This section examines the diets of bats at the two roosts in the two years following the slaughter to characterise them. We predicted that dung dependent *Aphodius* consumption should fall at the Dean Hall because of the FMD slaughter, but not at the Woodchester roost. The nearest slaughter of livestock to the Woodchester roost was at North Nibley, and near Berkeley, at least 6km away.

3.2 Methods

Weekly samples of bat droppings were collected from the maternity roosts at Dean Hall and Woodchester over the summers of 2001 and 2002, using the identical protocol described in Part 2.

Data for weeks 7 to 11, when bats would normally have eaten large amounts of *Aphodius* beetles, were combined for each roost separately and compared by roost and summer (year) using Mann-Whitney non-parametric tests.

3.3 Results

3.3.1 Dietary content by year, site and season compared

Figures 6 and 7 illustrate the total summer diets at the two roosts in the two summers following the FMD slaughter. They should also be compared with figures 1 and 2.

Figures 7 and 8 illustrate the diets for weeks 7 to 11 at the two roosts for these summers. They should be compared with weeks 3 and 4.

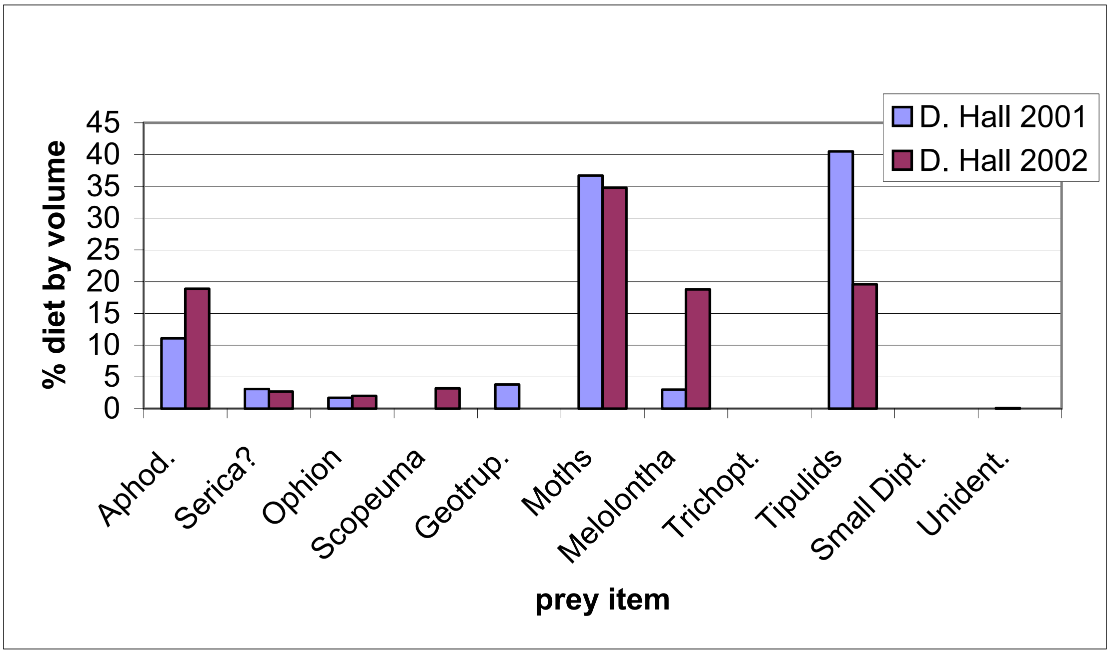

Figure 6: Total summer diet at Dean Hall in the two years after foot & mouth slaughter

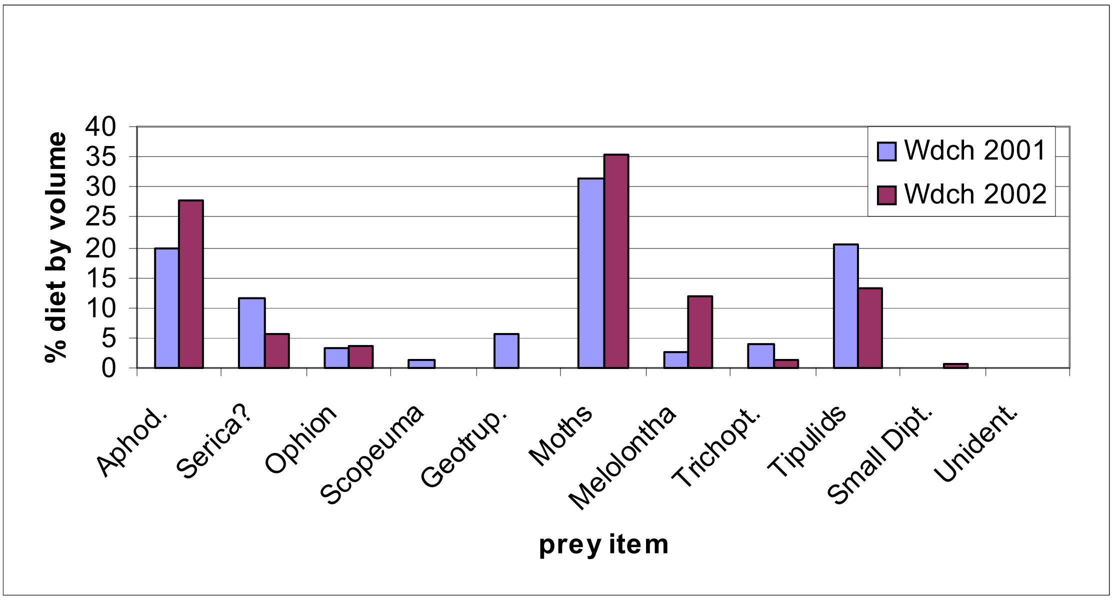

Figure 7 Total summer diet at Woodchester in the two years after Foot & Mouth slaughter

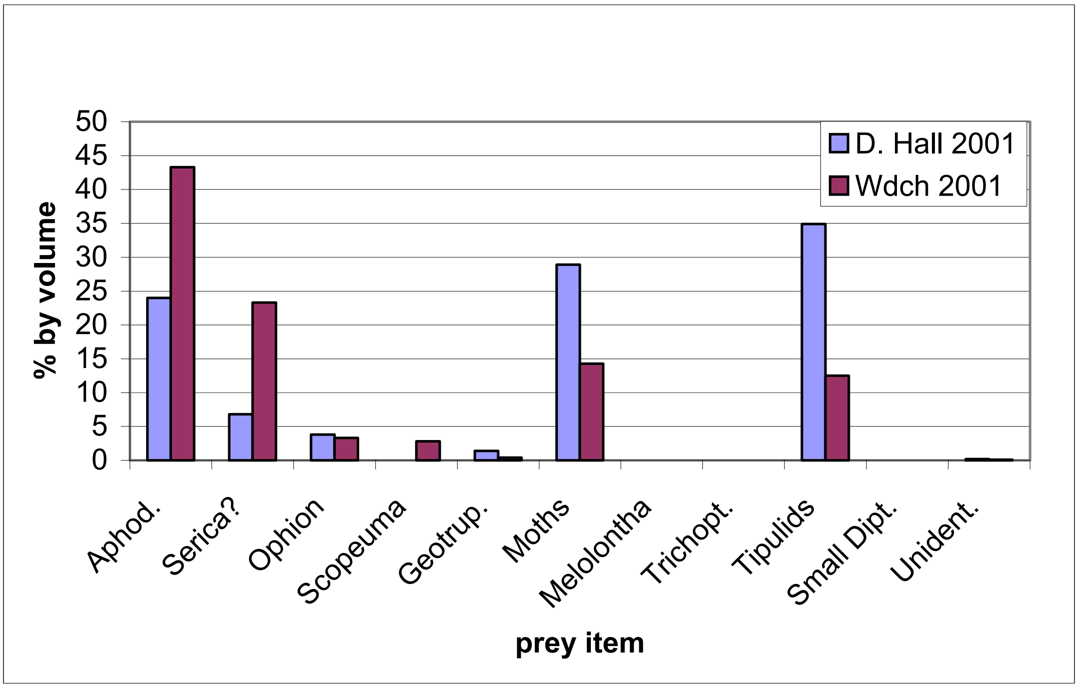

Figure 8 Summer diet for weeks 7 to 11 at the two roosts in 2001

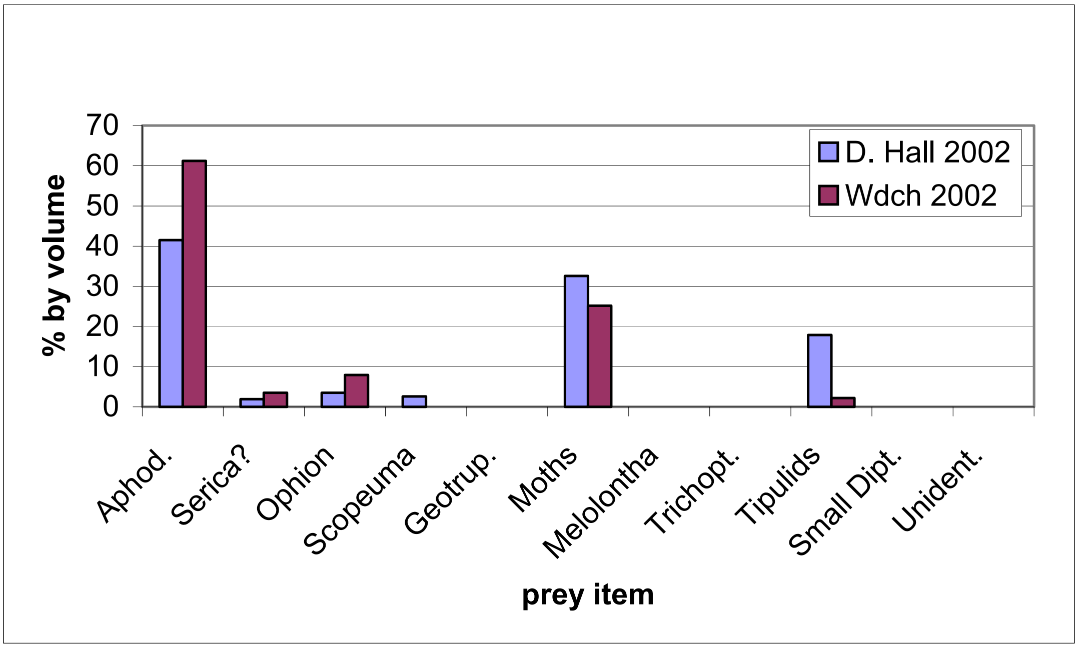

Figure 9 Summer diet at the two roosts for weeks 7 to 11 in 2002

Table 2 summarises the significant dietary differences between samples at the two roosts collected over the two summers.

Table 2 Significant prey consumption differences between Dean Hall and Woodchester bats post FMD for weeks 7 to 11 (Mann-Whitney tests)

Roost	Year	Variable	Sample size	Median	W	P (adj)
Woodchester	2001	Aphodius	60	9.30	3993.0	0.0407
Dean Hall	2001	Aphodius	60	0.00	"	"
Woodchester	2001	Moths	60	0.00	3212.5	0.0145
Dean Hall	2001	Moths	60	12.90	"	"
Woodchester	**2001**	**Tipulids**	**60**	**0.00**	**3034.5**	**0.0003**
Dean Hall	**2001**	**Tipulids**	**60**	**8.10**	**"**	**"**
Woodchester	2001	Serica?	60	0.00	3912.5	0.0339
Dean Hall	2001	Serica?	60	0.00	"	"
Woodchester	2002	Aphodius	60	58.40	4074.5	0.0175
Dean Hall	2002	Aphodius	60	31.60	"	"
Woodchester	**2002**	**Moths**	**60**	**0.00**	**3159.5**	**0.0076**
Dean Hall	**2002**	**Moths**	**60**	**24.70**	**"**	**"**
Woodchester	**2002**	**Tipulids**	**60**	**0.00**	**2981.0**	**0.0000**
Dean Hall	**2002**	**Tipulids**	**60**	**2.85**	**"**	**"**

NB. Data are arcsine transformed as for table 2.1. Arcsine data equivalent % figures are as follows: 0 = 0%; 2.85 = 0.5%; 8.1 = 2%; 9.3 = 2.5%; 12.9 = 5%; 24.7 = 17%; 31.6 = 27%; 58.4 = 72.5%. Bold data differences are significantly different ($p < 0.01$). The consumption of all other prey items in these two years was not significantly different. Grey shading demarks the two summers.

3.4 Discussion

After FMD slaughter significant differences in the consumption of four prey items between the two roosts were detected in 2001 and three items in 2002 (table 2). The prey were *Aphodius* beetles, moths and tipulids in both summers, with the addition of a scarabaeid beetle, believed to be a summer chafer, either *Serica brunnea* (L), or *Amphimallon solstitialis* (L.), in 2001. Consumption of *Aphodius* was reduced at both roosts, but was higher at Woodchester than at Dean Hall in that year. Data showed the opposite situation for moths. The differences seen previously only in 1998, were accentuated in the post slaughter period. At Dean Hall bats switched from mainly eating *Aphodius* to moths, and especially tipulids. At Woodchester bats ate higher amounts of *Serica* (or *Amphimallon*) rather than tipulids. In summer 2002 there was a recovery in the levels of *Aphodius* consumed at both roosts, but the differences in consumption at the two sites diverged. Differences for moth and Tipulid consumption also increased over 2001 to significant levels.

4. Comparison of summer diet of bats at Dean Hall and Woodchester Mansion before and after the slaughter

4.1 Introduction

In this section we compare data from the pre and post FMD slaughter summers in order to obtain an overall assessment of its impact upon the diets of the bats at the two roosts.

4.2 Methods

We used data generated using the methods in sections 2 and 3 above. Mann-Whitney non-parametric statistics were used to compare data before the slaughter with those after the slaughter at each roost separately. Only weeks 7 to 11 were compared, as these weeks cover the period when dung-dependent *Aphodius* beetles are normally eaten.

4.3 Results

Figures 10 and 11 illustrate the changes in summer consumption of dung-dependent insect prey items over the six years of the study. Summer 1995 is excluded for the reasons explained in Part 1. However, Figure 1 suggests that the data would have been similar to those from 1996.

The dung fly *Scatophaga* (= *Scopeuma*) is only eaten by these bats under stressed circumstances, particularly at certain times of the winter (Ransome 2002). As it is a daytime flyer, the bats presumably glean it from vegetation at night.

Different species of large dung beetles that belong to the genus *Geotrupes* fly mainly from late August through winter to April. Although the genus is an important key prey in winter and spring, it usually only shows up in the diet during cold springs (such as 1996 and 1998) under the protocol timings used.

The main dung-dependent insect that is normally consumed in large amounts is the beetle *Aphodius rufipes*. The Dean Hall data shows that the minimum consumption occurred in

2001, falling to about 10% of the total diet the summer after the FMD slaughter. However, in the following summer the level returned to normal pre-slaughter levels of just below 20%.

At Woodchester there was a decline in 2001 to just below 20%, followed by an increase to 27% in 2002. This is still well below the 36 to 38% levels of 1997 and 1998, but above the 1995 and 1996 levels. Those summers were affected by a long drought during July and August 1995 (Figure 11).

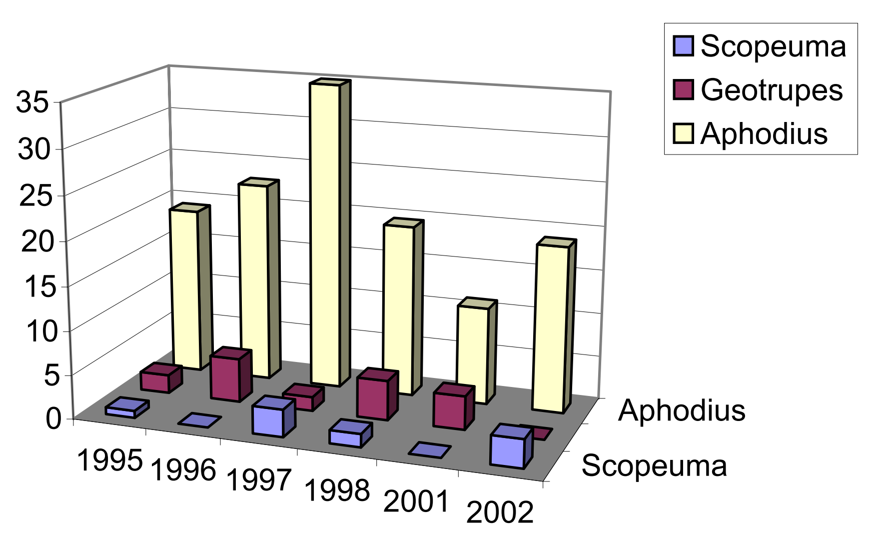

Figure 10 Dean Hall: percent dung-dependent prey in the summer diet by year of study

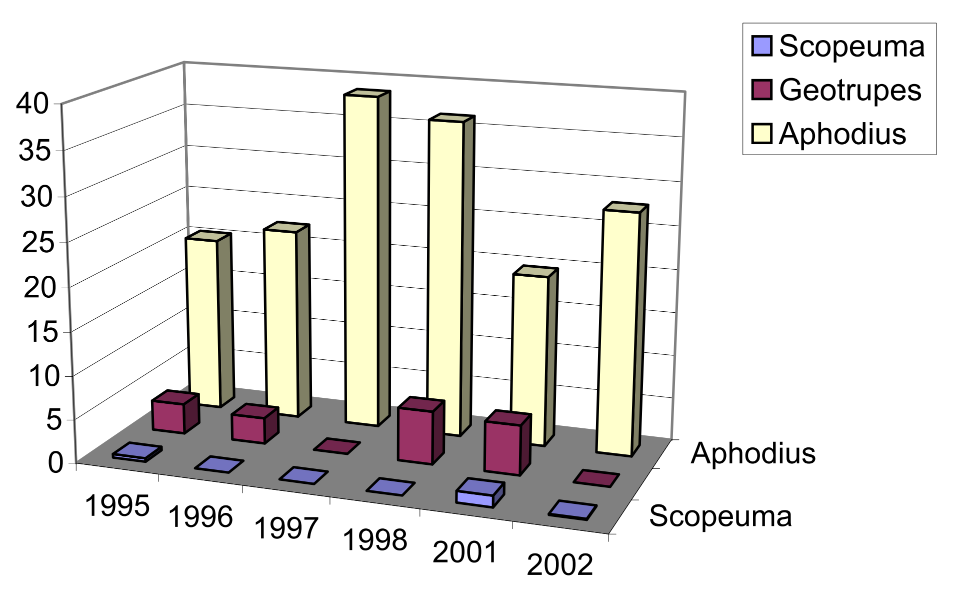

Figure 11 Woodchester: percent dung-dependent prey in the summer diet by year of study

4.3.1 Comparison of dietary content at the two roosts for weeks 7 to 11 before and after the slaughter

Dean Hall roost

Table 3 Significant differences in insect prey consumption by Dean Hall bats: pre and post FMD slaughter periods

Roost	FMD Period	Variable	Sample size	Median	W	P (adj)
Dean Hall	**Pre**	**Aphodius**	**180**	**45.00**	**30261.5**	**0.0000**
Dean Hall	**Post**	**Aphodius**	**120**	**15.65**	“	“
Dean Hall	**Pre**	***Tipulids***	**180**	**0.00**	**24218.0**	**0.0000**
Dean Hall	**Post**	***Tipulids***	**120**	**5.70**	“	“
Dean Hall	**Pre**	**Serica?**	**180**	**0.000**	**26223.0**	**0.0042**
Dean Hall	**Post**	***Serica?***	**120**	**0.000**	“	“

NB. Data from the same years as for table 4.1. Bold data are significantly different ($p < 0.01$). The pre FMD median for *Aphodius* of 45.0 equates to 50%, and the post FMD of 15.65 to 7.2%. The pre FMD median for tipulids of 0.0 equates to 0%, and the post FMD of 5.7 to 1%. The consumption of all other prey items in these two periods was not significantly different. *Serica* (or possibly *Amphimallon*) consumption increased significantly in the post FMD period.

Woodchester roost

Table 4 Significant differences in insect prey consumption by Woodchester bats: pre and post FMD slaughter periods

Roost	FMD Period	Variable	Sample size	Median	W	P (adj)
Woodchester	**Pre**	**Aphodius**	**180**	**67.2**	**29015.5**	**0.0078**
Woodchester	**Post**	**Aphodius**	**120**	**53.7**	**“**	**“**
Woodchester	**Pre**	**Serica?**	**180**	**0.000**	**25257**	**0.0000**
Woodchester	**Post**	***Serica?***	**120**	**0.000**	**“**	**“**

NB. Data are from 1996 to 1998 pre FMD, and 2001 & 2002 afterwards. Data were arcsine transformed before statistical tests were performed. The pre FMD median for *Aphodius* of 67.2 equates to 85%, and the post FMD to 65% of the diet. Bold data are significantly different ($p < 0.01$). The consumption of all other prey items in these two periods was not significantly different. *Serica* (or possibly *Amphimallon)* consumption increased significantly in the post FMD period, but the median data were identical.

4.4 Discussion

In Part 2 it was shown that the summer diets of bats at the two roosts were remarkably similar for years 1996 and 1997 prior to the slaughter. It seems likely that 1995 diets were also very similar, but data were not statistically tested.

Significant differences in the consumption of two prey items between the two roosts were detected in only one of the three summers statistically sampled (1998). The prey concerned were *Aphodius* beetles and moths. Consumption of *Aphodius* was higher at Woodchester than at Dean Hall in that year, and vice versa for moths. This may have been due to very high levels of moths in the Forest of Dean that year, or to the removal of cattle from fields close to Dean Hall that were present in earlier years. No similar occurrence took place at Woodchester (table 3), where grazing regimes maintained a steady improvement in *Aphodius* consumption year on year between weeks 7 to 11 of each summer from 1996 to 1998 (Figures 3 to 5).

The Dean Hall pre and post slaughter data (table 3) are consistent with the predicted impact of the serious reduction in fresh dung available to dung dependent insects in the Forest of Dean after spring 2001. *Aphodius rufipes* beetles that emerge from pupae need to build up their protein levels for muscle and egg production over many weeks (White 1960). Adult beetles have weak mouthparts that require them to feed on semi-liquid dung, such as that provided by fresh cattle dung. They could not do so in the Forest of Dean that summer in the absence of cattle. They are likely to have died from either an absence of dung, or high levels of competition for the limited amount of fresh dung available.

A major reduction in *Aphodius* consumption during weeks 7 to 11 in 2001 and 2002 by Dean Hall bats followed the spring 2001 slaughter of grazers. They switched to eating significantly more tipulids and *Serica* (or *Amphimallon*) instead. Both of these are secondary prey. These diet changes are consistent with the foraging hypothesis presented in Part 2.

Woodchester bats, although outside the actual FMD slaughter area, were also affected by poorer *Aphodius* levels in 2001 (table 4). They showed a significant fall in *Aphodius* consumption compared with the pre FMD slaughter, and ate more *Serica* (or *Aphimallon*) as did bats at Dean Hall. This was unexpected as the roost was outside the slaughter area.

One hypothesis for these findings is as follows:

Large populations of Aphodius beetles scattered widely over large areas are not profitable prey for foraging greater horseshoe bats. However, when herds of cattle are kept on grassland within the sustenance zone of a maternity roost, their fresh dung attracts concentrated beetle swarms that these bats can exploit.

The reasons supporting this hypothesis are listed below:

- Prior to FMD, large populations of *Aphodius* were generated across a wide area of the Forest of Dean by its highly favourable grazing regimes. Many cattle, sheep, deer and horses were grazed all-year-round in deciduous woodland interspersed by grassy regions. This included about 7,000 sheep and 500 deer that roamed freely around the extensive areas owned by the Forestry Commission. Although cattle dung is preferred in exposed situations, such as open fields, Landin (1961) showed that the dung of sheep, horses and deer were particularly effective as food sources capable of sustaining high populations of these beetles within forests.
- Landin also showed that *Aphodius rufipes* beetles can fly at least 10km to reach fresh dung supplies, attracted by its odour (Landin 1968). Since adult beetles need to feed on liquid dung that soon dries out in exposed situations, they constantly have to search for fresh dung sources that they must leave within a day or two. This constantly exposes them to bat predation (see review by Ransome 1996).
- The considerations above suggest that these beetles may normally be drawn to the foraging areas used by Woodchester bats from very large populations generated by surrounding grazed regions, such as the Severn Valley and even the Forest of Dean. They would be attracted by fresh dung from cattle kept in the Woodchester valley and surrounding farmland, under management agreements, from mid July to the autumn. Although the cattle grazing regimes near Woodchester Mansion were not affected during 2001 and 2002, the FMD slaughter resulted in the loss of many grazers within the Severn Valley, especially around Berkeley, during the summer of 2001.
- The slaughter of all of the sheep and cattle in spring 2001 around Dean Hall could not have prevented the emergence of large numbers of adult *Aphodius* beetles in the summer of 2001, since they would have developed from eggs laid in fresh dung the year before. It should have been summer 2002 before the lack of dung had its full effect on beetle populations. However, the reduction in *Aphodius* consumption by Dean Hall bats was greatest in 2001, showing a partial recovery in 2002 (see table 3.1 and figs 8 & 9). The re-introduction of some 2,000 sheep to the Forestry Commission's land in spring 2002, and of other grazers elsewhere in and around the Forest, would have helped to restore *Aphodius* populations. In addition, the deer population rose to about 800 by the summer of 2003.
- The production of fresh dung by local herds and flocks of grazers seems to be essential to concentrate these beetles into the dense swarms that bats can profitably exploit. Duvergé (1997) noted that when cattle were introduced into a field that

previously was not being used by these bats, on the first night afterwards, bats would forage over the field.

5. Quantity of insect prey eaten at Dean Hall and Woodchester Mansion before and after the slaughter

5.1 Introduction

Parts 2 to 4 above concentrated on the diet content of bats from the two maternity roosts. In this part we consider the amount of insect prey consumed, using dry dropping data to estimate consumption. Foraging success levels by bats has long been assessed from the dry mass of faecal pellets, or droppings, produced by colonies or individuals over time (Ransome 1973, 1997b, 2002, Kunz 1974). Dry droppings normally consist of about 70-80% indigestible insect exoskeletal fragments, especially when beetles are eaten. However, when only large moths are eaten, the level may fall to 35% (personal data). The remainder is soluble matter, including salts.

Dry dropping production per bat can be calculated in two ways. Firstly from collections of droppings from beneath a bat colony over a known time period, normally days or weeks. Secondly from collections from individual bats held in clean cloth bags for a maximum of a few hours.

In order to place the mean dry dropping production per bat per day (F) from colonies in context, it is necessary to consider the normal range of bats through the summer prior to the FMD outbreak. Ransome (1973) presented data for the summers of 1967 and 1970 for Woodchester bats. F levels of 0.43g/bat/day (= 430mg) were regarded as normal, with a fall to 220mg/bat/day in late pregnancy followed by a rise to about 450mg/bat/day through lactation. However, table 5 below shows F levels in Woodchester bats remained high at about 600mg/bat/day for the whole of the lactation period in 1997. These differences in F levels may be at least partly explained by different ratios of moths to beetle consumption. Dean Hall bats showed a similar pattern to the old Woodchester data.

5.2 Methods

As previously stated, the colony at Dean Hall has only been captured once. Hence only dropping collections from beneath the two colonies, as described in part 2, were used in this comparative study. Dusk exit counts were made prior to each weekly dropping collection (see part 8 below), so that the mean number of bats flying out to forage could be determined for each week of the diet study.

Wet droppings were bagged up and samples were dried to constant mass to determine the total dry mass for each week. Using the mean number of bats from the two exit counts made before and after each week, the mean dry mass of droppings per bat per day was calculated for the years 1997, 2001 and 2002.

5.3 Results

Data are shown in tables 5 to 7, and figures 12 to 14.

Table 5 Mean foraging success by bats at Woodchester and Dean Hall during the lactation period in 1997

YEAR		WOODCHESTER	DEAN HALL	F Ratio
1997	Week	Mean F (diet)	Mean F (diet)	
Early lactn.	6	523 (moth)	260 (moth/Aph/tip)	2.01
mid/late lactn.	7	620 (Aph)	492 (Aph/moth/Ser)	1.26
“	8	600 (Aph/moth)	535 (Aph/moth)	1.12
Mean F during Lactation		581	429	1.35

NB Foraging success is assessed from F: mean dry dropping production per bat per day (mg/bat/day). F ratio is mean F for Woodchester divided by mean F for Dean Hall. Mean F during lactation is the mean of weeks 6 to 8.
Diet abbreviation key: tip = tipulids; Aph = *Aphodius;* Ser = *Serica* (or *Amphimallon*).
The sequence in brackets indicates abundance order. For example in week 6 at Dean Hall moths were a major diet component, followed by *Aphodius* and tipulids. Only prey that formed more than 15% of the diet were listed.

Table 6 Mean foraging success by bats at Woodchester and Dean Hall during the lactation period in 2001

YEAR		WOODCHESTER	DEAN HALL	F ratio
2001	Week	Mean F (diet)	Mean F (diet)	
Early lactn.	6	360 (moth)	400 (moth/tip)	0.90
mid/late lactn.	7	583 (Ser/moth)	297 (moth/Ser)	1.96
“	8	726 (Ser/Aph)	437 (moth/Aph)	1.66
Mean F during Lactation		556	378	1.47

NB Foraging success is assessed from F: mean dry dropping production per bat per day (mg/bat/day). F ratio is mean F for Woodchester divided by mean F for Dean Hall. Mean F during lactation is the mean of weeks 6 to 8.

Diet abbreviation key: tip = tipulids; Aph = *Aphodius;* Ser = *Serica* (or *Amphimallon*).
The sequence in brackets indicates abundance order. For example in week 6 at Dean Hall moths were a major diet component, followed by *Aphodius* and tipulids. Only prey that formed more than 15% of the diet were listed.

Table 7 Mean foraging success by bats at Woodchester and Dean Hall through the lactation period in 2002

YEAR		WOODCHESTER	DEAN HALL	F ratio
2002	Week	Mean F	Mean F	
Early lactn.	6	496 (moth/Ser/tip)	311 (moth/Ser/Dfly)	1.59
mid/late lactn.	7	557 (moth/Aph)	282 (moth/Aph)	1.98
“	8	490 (Aph/moth)	289 (moth/Aph)	1.70
Mean F during Lactation		514	294	1.75

NB Foraging success is assessed from F: mean dry dropping production per bat per day (mg/bat/day). F ratio is mean F for Woodchester divided by mean F for Dean Hall. Mean F during lactation is the mean of weeks 6 to 8.

Diet abbreviation key: tip = tipulids; Aph = *Aphodius;* Ser = *Serica* (or *Amphimallon*).

The sequence in brackets indicates abundance order. For example in week 6 at Dean Hall moths were a major diet component, followed by *Aphodius* and tipulids. Only prey that formed more than 15% of the diet were listed.

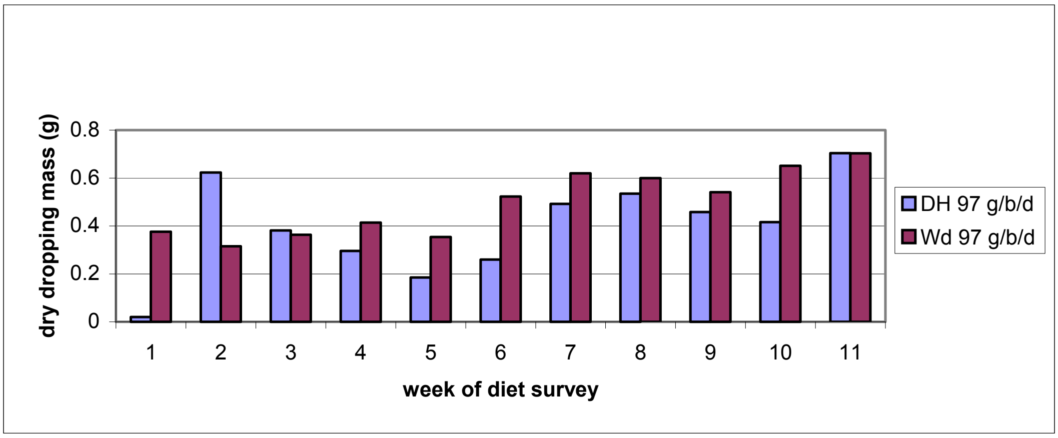

Figure 12 Daily dry dropping mass per bat per day by week and roost in 1997

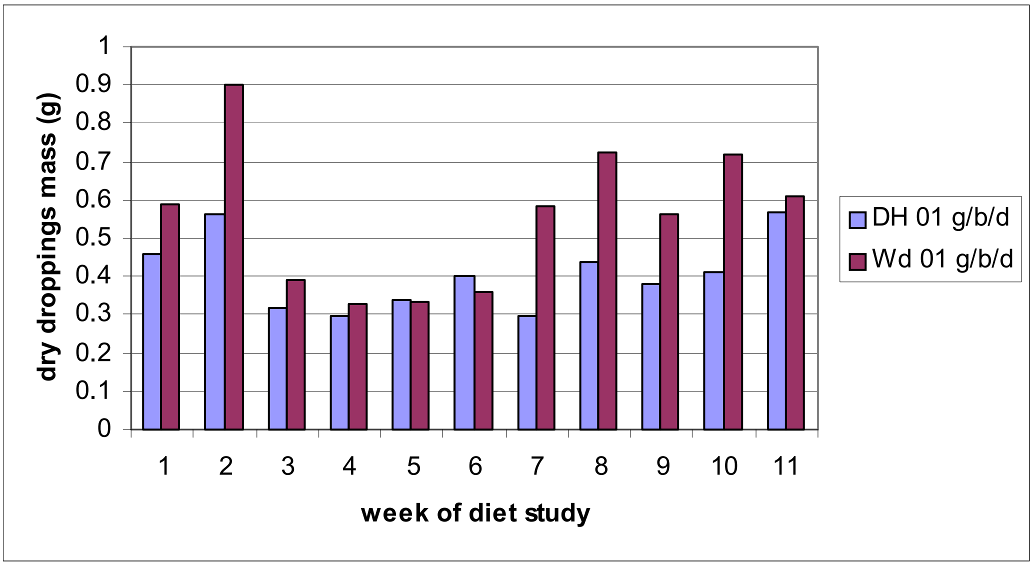

Figure 13 Daily dry dropping mass per bat per day by week and roost in 2001

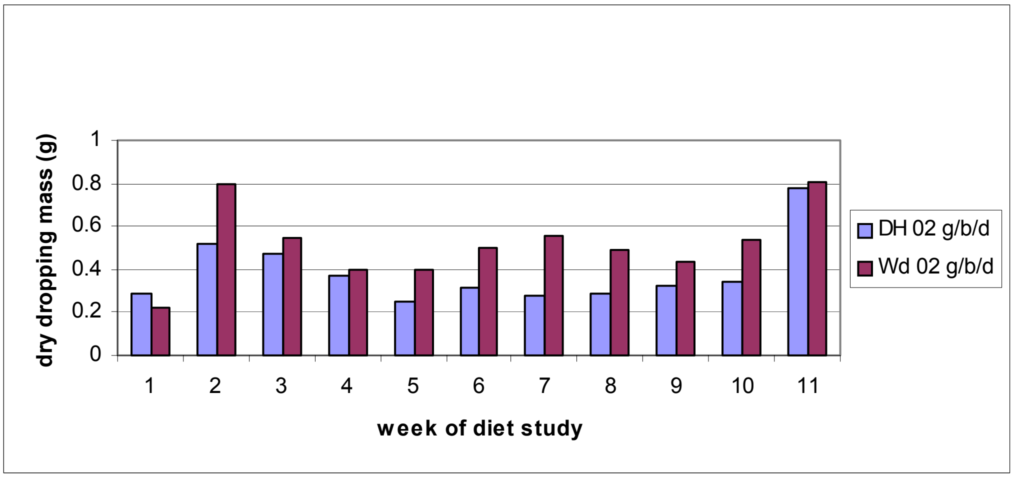

Figure 14 Dry dropping mass per bat per day by week and roost in 2002

5.3.1 Dropping production levels at Woodchester and Dean Hall in 1997 and after FMD slaughter

F levels at Woodchester and Dean Hall in 1997

Table 5 shows data for one year prior to FMD (1997) over the lactation period. This is likely to be the most critical part of the summer, since it affects the growth and survival of the young. In early lactation that year, Woodchester bats ate lots (523mg/bat/day) of moths, their key prey. Later on they ate 600 to 620mg/bat/day of *Aphodius* and *Aphodius*/moths. These differences in F may be purely due to the switch from moths to *Aphodius*. At Dean Hall, in early lactation, only 260mg/bat/day was eaten, when bats were feeding on three prey, including tipulids that are secondary prey. This low level, combined with mixed prey, suggests that the bats were diet stressed. Later in lactation F rose to 429 and 535mg/bat/day at Dean Hall as bats ate only key prey. As about 75% of Dean Hall bats were non-breeding, compared with about 50% at Woodchester, these slight consumption differences in late lactation could be explained by differences in the proportion of lactating bats.

F levels at Woodchester and Dean Hall after FMD slaughter

Tables 6 and 7 show data for 2001 and 2002 respectively over the lactation period. In 2001 mean F was 556mg/bat/day at Woodchester and 378mg/bat/day at Dean Hall, with the lowest levels (297mg/bat/day) at Dean Hall in week 7. Although about 75% of Dean Hall bats were non-breeding, compared with 50% at Woodchester, these consumption differences are unlikely to be explained by differences in prey consumed, or by the proportion of lactating bats.

5.4 Discussion

Ransome (1997b) estimated the dawn foraging success of individual bats at Woodchester, where they have been regularly captured and placed into clean cloth bags (method described in Jones and others 1995). Females form the bulk of this colony throughout the summer months. His main conclusions were as follows:

- Lactating females consume the most food in good weather in July and early August (about 480mg dry dropping per bat equivalent, or 0.48g/bat/dawn foraging bout).
- Pregnant and post lactating bats consume food equivalent to about 260mg/bat/dawn foraging bout.
- Immature female bats consume about 300mg dry dropping equivalent in good weather between June and late August (subsequent analyses for immature males show that they consume similar amounts, and adult males also - Ransome unpublished data).
- Severe weather, including cold spells and wet/windy conditions, severely depress consumption by all female groups to about 80mg per bat.

Duvergé (1997) showed that most sex and age groups, including lactating female bats normally forage three times each night from July. The bouts were after dusk, in the middle of the night, and before dawn. Dusk foraging bouts were longest, and so probably involved the consumption of the greatest amounts of food by each age and sex group. Dawn was next longest, and the bout in the middle of the night was the shortest. During lactation, the combined dawn and middle of the night foraging bouts lasted longer than the dusk bout under favourable weather conditions, and so overall may be more productive than the dusk bout alone. However, bats often night-roosted at other sites, and failed to return until dawn.

5.4.1 Relation between dawn foraging production data and F levels

Bats returning from dawn foraging bouts deposit all of their droppings onto the polythene sheets, or within cloth bags for the contained period, if captured. Bats that forage at dusk, may or may not return to the maternity roost for periods overnight, and deposit some of the droppings generated from dusk consumption onto the sheets.

Two extreme scenarios are possible:

- If all bats return to the maternity roost overnight except when foraging, F should be less than twice the dawn foraging production.
- If no bats return to the maternity roost overnight, F should equal the dawn foraging production alone.

NB. Both conclusions assume that all dusk prey remains have been egested before bats return from their dawn bout. However, dawn foraging production is likely to include some prey remains from the middle of the night foraging bout.

In actual fact the true state of overnight returns by bats will be somewhere in between these extremes, and changes with reproductive status. Immature, and pregnant female bats are more likely to stay out all night and use night roosts near their foraging grounds than lactating females. This is because the latter need to return to suckle their young, since these are not normally taken out of the roost.

As we have no clear data on the return levels of bats at each roost, we cannot compute a precise relationship between dawn foraging data and F levels.

However, F for bats in a maternity colony should never fall below the dawn foraging production levels described above, unless the bats present are failing to consume the normal amounts expected by their sex and reproductive status. This may be due to severe weather effects depressing capture or a lack of suitable prey for other reasons.

In 2002 mean F for weeks 6 to 8 was 514mg/bat/day at Woodchester and 294mg/bat/day at Dean Hall despite a considerable similarity in the prey consumed. These consumption differences are much greater than in 2001. The figure of 294mg/bat/day is typical of pre FMD non-breeding bat production after dawn foraging alone. Since lactating bats must have returned to suckle their young at intervals through the night, consumption levels by Dean Hall bats must have been seriously below normal levels throughout lactation in 2002.

Overall the data presented show that the diet deterioration that occurred after FMD slaughter at Dean Hall (parts 3 and 4) was linked to a significant fall in prey consumption over the late lactation period. Slight falls in prey consumption (F) at Woodchester may also be linked to the reduced importance of *Aphodius* in the diet there (table 4).

6. Winter diet of bats at Dean Hall and Woodchester Mansion after the slaughter

6.1 Introduction

Winter-feeding by greater horseshoe bats was first shown to occur during the hibernation period, that lasts from October to May, by Ransome (1968). As the incidence of mild weather increased, body mass-loss rates of bats through the winter decreased. This was marked in adult males, but also occurred in first-year bats. From these data it was argued that feeding could potentially have a significant influence on the survival of winter by these bats. Ransome (1971) showed that they were able to synchronise their arousals with warm days, rather than cold ones.

Radio-telemetry studies at Cheddar (Park, Jones & Ransome 1999, 2000) showed that most bats tend to synchronise their arousals with dusk, and their activity remains nocturnal throughout the hibernation period. They argued that, as dusk is normally the time when insect availability is greatest on a particular day, and at a time when bats are able to forage, their findings support winter-feeding by this species.

Two different ways of investigating winter diet and the amounts consumed have been used (Ransome 2002). One is to visit the maternity roost through the winter and collect droppings as in the summer (part 2). Greater horseshoe bats erratically return to their maternity roost for short periods overnight through the winter. The other is to catch bats within hibernacula, place them into bags, and collect the droppings from the bags. This part considers data from roosts, and part 7 considers data from hibernacula.

6.2 Methods

Faecal samples were collected at monthly intervals from the two maternity roosts over the winters of 2001/2 and 2002/3 between October and April. A total of 14 samples per roost were collected in total over these two winters. Previously a similar study by Ransome (2002) took place in winters 1997/8 and 1998/9, but only at Woodchester Mansion. Droppings fell onto thick plastic sheets that covered the area beneath each incubator system.

On each occasion that each attic roost was entered, droppings were collected by hand and placed into a polythene bag. Great care was taken not to compress them into a mass, as single pellet analysis was required for this study. Afterwards each sheet was swept clean to ensure that no contamination of the next sample could occur.

The droppings collected were from bats of unknown age and sex.

Droppings were dried to constant mass as in part 5, and analysed for diet content as in part 2.

6.3 Results

Figure 15 shows dry weight data for five years through the slaughter period for Woodchester bats. Equivalent data for Dean Hall were not obtained.

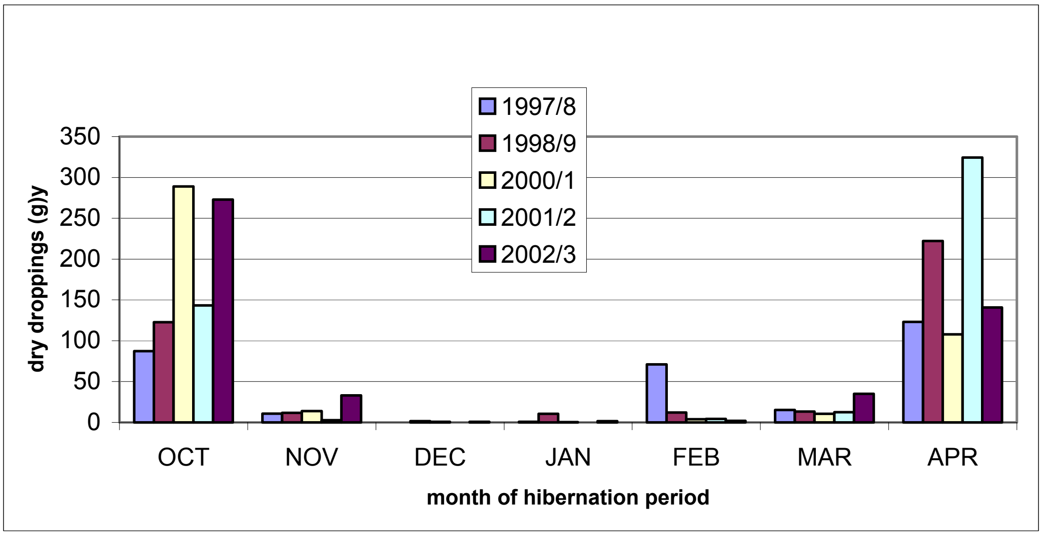

Figure 15 Dry weight of droppings collected monthly over winter at Woodchester before and after FMD

Table 8 summarises the dry dropping production data obtained for the two winters after FMD for both roosts.

Table 8 Weights of dry droppings per month at the two roosts during the two winters after FMD slaughter

Month of winter	**Dean Hall 2001/2 (g)**	**Woodchester 2001/2 (g)**	**Dean Hall 2002/3 (g)**	**Woodchester 2002/3 (g)**
October	1190	143.2	532	273
November	251.3	2.8	792.6	33.1
December	0	0	115	0.7
January	0	0	23	1.7
February	21.5	4.2	53	2
March	15.3	12.5	31	35
April	201	324.4	102	141
Totals	**1679**	**487**	**1649**	**486**

Figure 15 illustrates data for Woodchester bats over a five year period, three of them prior to FMD slaughter. No similar data were available for Dean Hall bats.

Figures 16 and 17 illustrate the data in table 8 by year at the two roosts.

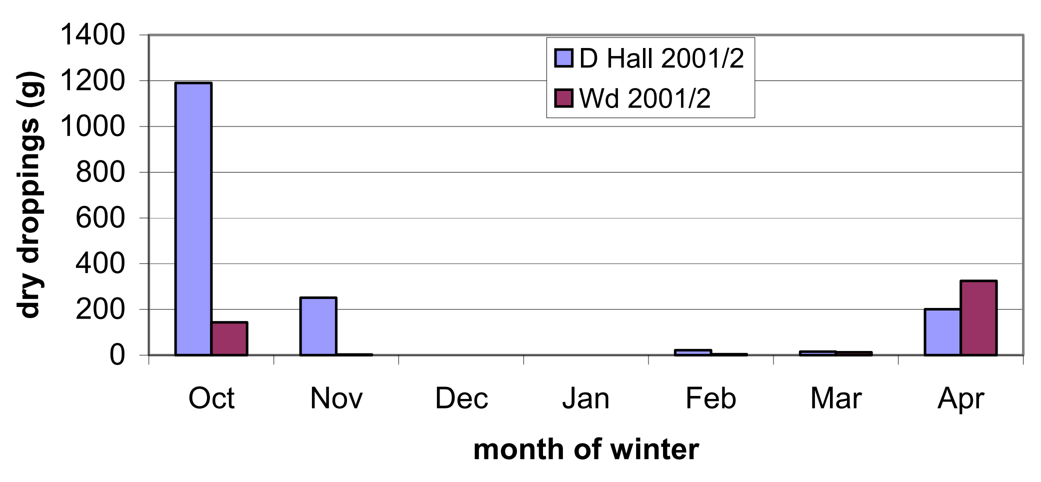

Figure 16 Dry weight of droppings per month at the two roosts in winter 2001/2

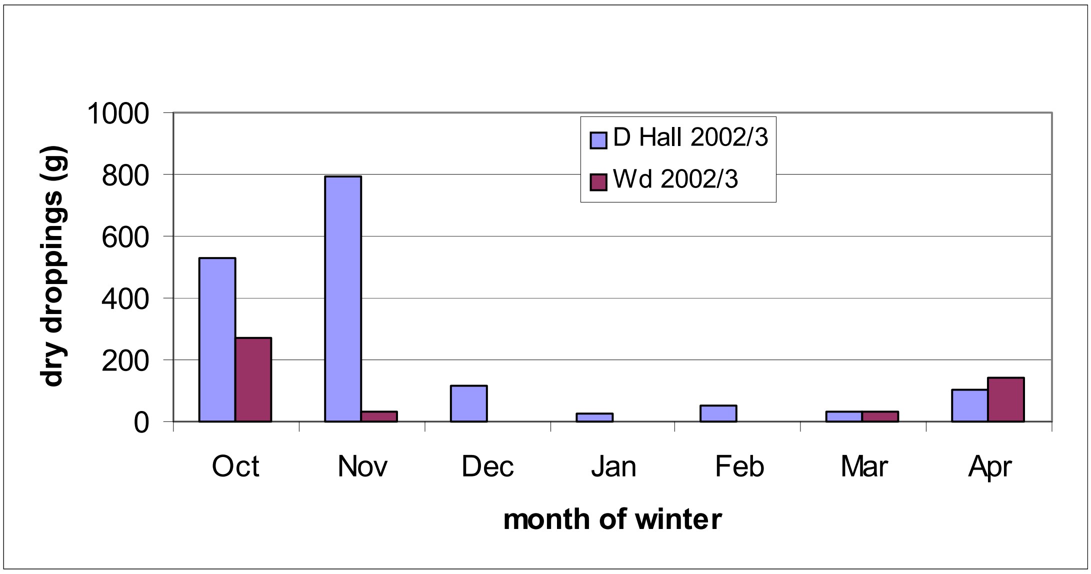

Figure 17 Dry weight of droppings per month at the two roosts in winter 2002/3

Figures 18 and 19 illustrate the October to April diet content of the two roosts in the two winters following FMD slaughter.

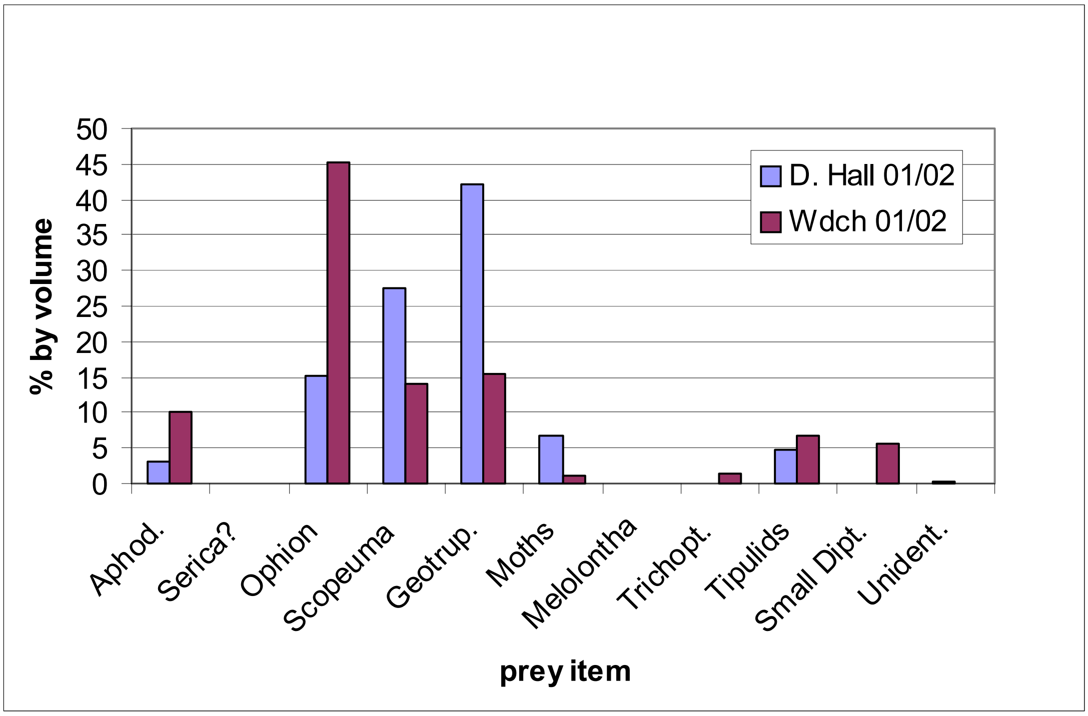

Figure 18 Winter diets at the two breeding roosts in winter 2001/2

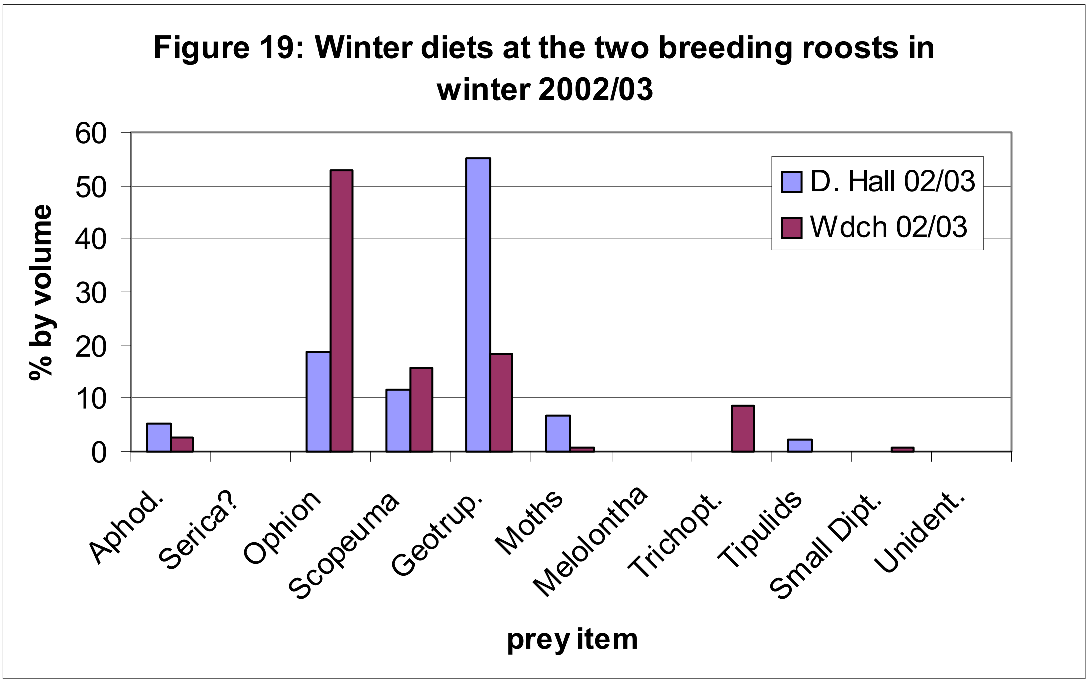

Figure 19: Winter diets at the two breeding roosts in winter 2002/03

6.4 Discussion

Fat deposition by this species normally occurs rapidly over a ten-day period between late September and mid October, according to age and sex group (Ransome, unpublished data). Mature females tend to store fat earlier than other groups, and acquire higher reserves. Mature males normally start the winter with the lowest levels, especially if they hold mating territories with a large harem (Ransome 1991). They usually need to feed extensively in winter. First year bats, or young of the year, are the last to leave the breeding roost, especially in years when births are late, possibly because they still have important growth processes to complete. They often leave significant fat deposition until late in October.

If autumn weather is poor, as it was in October 1998, the body reserves of all sex and age groups at the start of hibernation may be insufficient for survival to the next spring without some winter-feeding.

Table 8 shows that in both winters after FMD, Dean Hall bats generated much higher levels (over three times as much) of dry droppings in October and November, than the Woodchester bats. At this time first year bats would have been the dominant age group using the roost. They should have deposited much of their fat reserves at this time.

In March and April, the Woodchester bats produced slightly more droppings than the Dean Hall bats (table 8). The Woodchester roost is usually occupied by a mixture of first year bats and adult females at this time. Both would have been close to their minimum fat reserve levels at the end of the winter (Ransome 1968). Successful feeding at this time would be important to both bat populations to avoid starvation and start pregnancy (Ransome & McOwat 1994).

The total weight of dry droppings at each of the two roosts was consistent for the two winters. In the pre FMD winters for Woodchester, total data were 308g (1997/8); 394g (1998/9); 426g

(2000/1), compared with 487g and 486g in the two post FMD winters. The amounts rose in line with population increases over these years until FMD, when they stabilised.

Figure 15 shows that the pattern of Woodchester winter data before FMD, though erratic, was essentially similar to that afterwards.

Figures 18 and 19 show the total winter diet for the two winters following FMD slaughter. The diet for Woodchester bats in the two winters was similar to data obtained in 1997/8 and 1998/9 (Ransome 2002). *Ophion* wasps were a major constituent (46% and 53%), with small amounts of *Geotrupes* dung beetles (16% and 18%) and the dung fly *Scatophaga* (= *Scopeuma*) in both winters.

The diet of Dean Hall bats was dominated by *Geotrupes* beetles (42% and 55% in the two winters). Dung flies were next important in 2001/2, followed by *Ophion* wasps. In 2002/3 *Ophion* wasps were the second most common winter prey, followed by dung flies.

Since no pre FMD data were available for Dean Hall, we cannot comment on possible changes from previous levels. However, the diet of the Dean Hall bats for both winters since FMD have shown superior levels of the key prey *Geotrupes*, to that of Woodchester bats. Although *Geotrupes* depends on supplies of winter dung from grazers, the FMD slaughter did not result in a catastrophic fall in consumption to the low levels that are normal at Woodchester. This was not anticipated.

7. Winter diet of bats at Buckshaft and Lords Wood hibernacula before and after the slaughter

7.1 Introduction

Greater horseshoe bats that have fed well in summer may take over 10 hours to process the insects they caught just before dawn. Dropping production rates from such bats are rapid in the first few hours, and taper off gradually until late afternoon (Ransome 1978). If these bats become torpid, due to low ambient temperature conditions within the roost, and/or low food consumption, egestion of the final droppings from dawn foraging is delayed. Just before dusk such bats arouse and increase their dropping production rates again whilst they groom and urinate just prior to leaving the roost to forage.

In winter, bats that have fed after arousing from torpor may enter their next torpor bout with substantial amounts of skeletal remains still retained within the gut. On their next arousal, normally at dusk, these bats also defaecate before leaving to try to forage again.

Torpid winter bats that are captured and handled may egest droppings. If they do, it indicates successful foraging occurred after their previous arousal. Collections of droppings from bats held in clean bags after winter capture, allow both the quantity of prey consumed, and the diet to be investigated.

7.2 Methods

Clusters of bats were caught within two important winter hibernation sites in the Forest of Dean that had been studied previously (Ransome 2002). They were at Buckshaft near

Cinderford, and Lords Wood near Symonds Yat. Each bat was placed into a clean bag before it was processed. Any droppings produced were collected, dried, weighed and analysed for diet content. Ransome (2002) provides more details of the methods used.

7.3 Results

Tables 9 to 15 below summarise the masses of dry droppings collected from individual bats using tables as in Ransome (2002). Each table refers to a different date. Data are either repeated from Ransome (2002), or obtained during the current study as indicated.

Buckshaft, Cinderford

Data prior to FMD slaughter are shown in tables 9 and 10. Temperature data for Dursley, collected by RDR, are also provided. Dursley is about 16km from Cinderford. In December 1998 (table 9), a large cluster of 64 bats, included 24 adult males. Several bats produced large amounts of droppings. Ransome (2002) estimated that 20mg of droppings from a torpid bat reflected total dropping production from prey consumed of about 286mg. This is the mean figure for non-lactating female bats in summer (Ransome 1997b). The equivalent estimate for 30mg from a torpid bat is 429mg. This is close to the mean for lactating females. Hence in December 1998, 2 first-year males, 1 second-year male and 2 mature male bats, or about 8% of the cluster, had consumed large amounts of prey during their last foraging bout. They ate mainly *Geotrupes* beetles. Some 45%, or 31 bats, had eaten nothing after their previous arousal.

In December 1999 consumption levels by 24 bats from a small cluster lacking mature males are shown in table 10). About 21% had consumed large amounts of beetles and 46% had eaten nothing. The milder weather prior to capture may have made very profitable foraging easier that winter.

Table 11 shows that in December 2001, in the winter immediately following FMD slaughter, during another very mild spell, 11 bats (about 15%) of a large cluster of 75 bats had fed very well. The bats, mostly mature males, had eaten mainly *Geotrupes* beetles as before the slaughter (table 16). Only 24% had eaten nothing.

The second winter (table 12) after the slaughter, the cluster caught was much smaller. Only 46 bats were caught, and few adult males were present. Only about 2% had eaten large amounts of prey, and about 70% had eaten nothing. This may have been due either reduced *Geotrupes* beetle availability, or to the much colder spell of weather prior to capture. Those bats that had fed, showed high *Geotrupes* levels as previously (table 16).

Table 9 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 6 December 1998

Dursley the previous day: maximum temperature = 1.9 ^{o}C; minimum temperature = -4.6 ^{o}C; no overnight rain; wind 1 NW. 3 days >10 ^{o}C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	4	10	4	4	9	0
1-5	3	0	2	1	5	2
6-10	1	1	1	0	4	0
11-15	0		1	1	0	1
16-20	0		0	0	1	
21-25	0		0	0	2	
26-30	0		0	1	1	
31-35	0		0		0	
36-40	1		0		1	
41-45	0		0		0	
46-50	1		1		0	
Over 50					1 (51mg)	

Source (Ransome 2002) Total 64 bats, 24 mature males.

Table 10 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 12 December 1999

Dursley the previous day: maximum temperature = 10.7 ^{o}C; minimum temperature = 3.4 ^{o}C; no overnight rain; wind 4 NW. 5 days >10 ^{o}C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	5	3	2	1		
1-5	1	3	0			
6-10	0	2	0			
11-15	0	0	0			
16-20	0	0	0			
21-25	0	1	0			
26-30	1	1	0			
31-35	2	0	0			
36-40		0	0			
41-45		2	0			
46-50			0			
Over 50			1 (57mg)			

(Source Ransome 2002) Total 24 bats, no mature males.

Table 11 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 9 December 2001

Dursley the previous day: maximum temperature = 5.2 °C; minimum temperature = -1.2°C; no overnight rain; wind 1 N. 7 days >10 °C in the last ten days

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	6	7	0	4	1	
1-5	3	2	1	1	1	
6-10	3	2	0	1	5	
11-15	1	2	1	0	3	
16-20	0	1	0	0	4	
21-25	6	1	1	0	1	
26-30	0	2	1	1	3	
31-35	0		1		2	
36-40	0				2	
41-45	0				1	
46-50	0				1	
Over 50	1 (52)		1 (77)		2 (60, 65)	

Source (Ransome, new data) Total 75 bats, 26 mature males

Table 12 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Cinderford 14 December 2002

Dursley the previous day: maximum temperature = 4.7 °C; minimum temperature = 0.5 °C; no overnight rain; wind 0. 1 day >10 °C in the last ten days.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	16	9	1	5	0	1
1-5	2	1	1		0	
6-10	2	1	0		2	
11-15	2		0		0	
16-20	0		0		0	
21-25	0		0		0	
26-30	1		0		1	
31-35			0			
36-40			0			
41-45			0			
46-50			1			
Over 50						

Source (Ransome, new data) Total 46 bats; 3 mature males

Lords Wood, Symonds Yat. A visit in February 1999 showed slight differences in dropping production to Cinderford bats prior to slaughter (table 13). Only one winter was sampled. Bats at Symonds Yat were present in much lower numbers, as was normal (previous data for over 5 years). Only one bat (about 5% of the total), an adult male, produced more than 30mg of droppings. About 55% of the bats produced nothing. Those that had fed, ate mainly *Geotrupes* beetles (table 17) as at Cinderford.

In February 2002, a year after the slaughter (table 14), a similar picture occurred. Only one mature male was present, however, in another cluster of 22 bats. The weather was much colder that February, and probably accounted for the small differences between data in tables 13 and 14.

In the second winter following the slaughter, in February 2003, after a milder spell in the previous 10 days, a larger cluster including 8 mature males was caught (table 15). About 17% produced large amounts of droppings, and only 43% produced none. Once again the main prey consumed were *Geotrupes* beetles.

Table 13 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Symonds Yat 23 February 1999

Dursley the previous day: maximum temperature = 7.7 °C; minimum temperature = -0.8 °C; no overnight rain; wind 3 NW. 6 of the last 10 days >10 °C.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	2	2	4	4	0	
1-5	1		0	1	0	
6-10			1	1	1	
11-15			1		1	
16-20					0	
21-25					2	
26-30					0	
31-35					1	
36-40						
41-45						
46-50						
Over 50						

(Source Ransome, new data). Total 22 bats, 5 mature males

Table 14 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Symonds Yat 11 February 2002

Dursley the previous day: maximum temperature = 11.2 °C; minimum temperature = 3.4 °C; heavy overnight rain; wind 5 W. 0 of the last 10 days >10 °C

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	11	5	0	1	0	
1-5	1		1		0	
6-10			0		0	
11-15			1		0	
16-20			1		0	
21-25					1	
26-30						
31-35						
36-40						
41-45						
46-50						
Over 50						

(Source Ransome, new data) Total 22 bats, 1 mature male

Table 15 Number of individual bats of different age and sex groups classified by mass of droppings produced after provoked arousal. Symonds Yat 13 February 2003

Dursley the previous day: maximum temperature = 6.3 °C; minimum temperature = 1.0 °C; no overnight rain; wind 0. 4 of the last 10 days >10 °C.

Dropping mass range (mg)	First year males	First year females	Second year males	Second year females	Second year plus males	Second year plus females
0	4	7	1	0	0	1
1-5	0	0	0	0	1	
6-10	1	0	1	0	2	
11-15	2	1	0	1	0	
16-20	0		0		0	
21-25	0		0		1	
26-30	1		0		1	
31-35			1		0	
36-40			0		1	
41-45			1		1	
46-50					0	
Over 50					1 (53)	

(Source Ransome, new data) Total 30 bats, 8 mature males.

7.3.1 Dietary content by winter and site compared

Tables 16 and 17 summarise the data for each site and winter.

Table 16 Diets of bats captured at Cinderford in December by winter before and after FMD slaughter

Prey item	6 December 1998	12 December 1999	9 December 2001	14 December 2002
Aphodius	15.8	0	0	0
Ophion	0	0.6	0	0.2
Scatophaga	3.4	3.3	0	0
Geotrupes	70.5	94.4	96.2	99.8
Moths	6.8	0	3.6	0
Small Diptera	3.5	1.7	0.2	0
N bats sampled	28	28	50	12

All data, apart from sample size are percentage of total diet.

Table 17 Diets of bats captured at Symonds Yat in February by winter before and after FMD slaughter

Prey item	23 February 1999	11 February 2002	13 February 2003
Aphodius	0	0	0
Ophion	27.8	0	0
Scatophaga	0	0	0
Geotrupes	61.1	92.5	91.9
Moths	11.1	0	7.6
Small Diptera	0	7.5	0.5
N bats sampled	10	4	16

All data, apart from sample size are percentage of total diet.

Both tables 16 and 17 show that the consumption of the dung beetle *Geotrupes*, the key prey identified by Ransome (2002) in winter, has remained very high after FMD slaughter within the Forest of Dean.

7.3.2 Dispersion of bats before and after FMD slaughter

Before FMD, it was noticeable from recapture data of ringed individuals, that many more Woodchester-born bats over-wintered in hibernacula within the Forest of Dean, rather than the reverse situation. Furthermore, it was primarily first-year bats from cohorts ringed at Woodchester the previous summer that were caught hibernating in clusters at Buckshaft. Movements of bats born at Dean Hall to hibernacula around Nailsworth, were mainly of sexually mature bats that occupied scattered territorial mating sites in October and April (Ransome 1991).

After FMD slaughter this pattern significantly changed as shown in table 18. In the winter of 2001/2, before dung-deprivation should have affected *Geotrupes* beetle populations, 3 first-year Woodchester bats wintered at Buckshaft. The following winter only one first-year bat wintered there. In contrast, for the first time, in the winter of 2002/3, five immature Dean Hall-born bats were found hibernating in type one and two cluster sites (Ransome 1991). Also, two Woodchester-born bats that previously hibernated in the Forest of Dean, used Nailsworth sites instead that winter.

Table 18 Movements of bats between the Woodchester/Nailsworth and Dean Hall/Forest of Dean areas by period before and after FMD slaughter

FMD period (summers)	N bats moving from Wdch/N'th to DH/FoD	N bats moving from DH/FoD to Wdch/N'th
Pre FMD (1993 to 2000) 8 years	22	8
Post FMD (2001 & 2002) 2 years	4	10
Totals	26	18

Wdch = Woodchester; N'th = Nailsworth hibernacula; DH = Dean Hall; FoD = Forest of Dean hibernacula.
Chisquare test on pre & post FMD data: χ^2 = 7.912; P value = 0.005; DF = 1.

The numbers of bats occupying the Buckshaft hibernaculum in the Forest of Dean provides further evidence for the impact of FMD upon the dispersion of bats. Prior to FMD the numbers there rose in parallel with those at Dean Hall, reaching 87 in winter 2000/01. The following winter 77 were found, and in 2002/3 they had fallen to 46 during the same winter that saw bats cross the River Severn to hibernate within Nailsworth mines. Other bats scattered in small numbers to other hibernacula in the Forest of Dean (DJP data).

The Nailsworth mine occupied by four of the Dean Hall bats in winter 2002/3, was adjacent to Minchinhampton Common, which is currently mainly a golf course, usually grazed by cattle only through the summer months. Due to restricted grazing during the summer of 2002 and the mild autumn, some cattle were left to graze the long grass until late November that year. The entrance feeding post of one mine had the remains of several *Geotrupes* beetles beneath it, with lots of fresh droppings in October that winter. This was the first time this had happened in several decades. In the early 1960s many fragments of these beetles, with substantial amounts of droppings, used to be found at the feeding posts at a time when a large herd of cattle was left to graze over the winter on the Common. At that time, as at Cinderford in the late 1990s, clusters of up to 80 bats hibernated in the mines, including many adult males. From the 1970s to the late 1990s there were only between 10 and 18 bats present in these mines through the winter.

7.4 Discussion

FMD slaughter seems to have had no significant impact upon the amount or frequency of *Geotrupes* beetle consumed by individual bats at the two hibernation sites within the Forest of Dean over the two following winters. This contrasts with data on *Aphodius* consumption at the Dean Hall summer roost. In the first winter, since adult beetles would have developed using dung produced by grazers before the slaughter, this was predicted. However, by the second winter (2002/3) an impact on bat’s diet was expected, but did not occur. However, bats seem to have maintained their high levels of *Geotrupes* consumption at least partly by dispersing away from their major cluster site at Buckshaft. Most bats probably only moved to other hibernacula nearby, but some travelled to mines in the Nailsworth area.

The data shown above confirms the suggestion made by Ransome (1968), that the foraging habitat outside a hibernaculum, as well as the thermal regimes within it, is an important factor controlling the numbers of bats present in winter. The low levels of winter greater horseshoe bat populations in the Nailsworth Mines seems largely to reflect the absence of significant grazers close to their entrances. This situation is contrasted by the very high numbers of lesser horseshoe bats present. They cannot feed on *Geotrupes* beetles.

Geotrupes beetles occur in small numbers (1-2) per cow-pat and other grazer’s dung, and do not swarm at fresh pats as *Aphodius* does. Since they are very large insects, bats probably catch them by either hawking or perch-feeding (Jones & Rayner 1989). Clearly enough *Geotrupes* beetles to allow successful foraging by small numbers of bats were sustained within the Forest of Dean by the fallow deer population of some 500 animals that had increased to over 800 by the summer of 2003, together with the 2,000 sheep and also cattle reintroduced to Forestry Commission land in the spring of 2002. By June 2002, about 47,000 sheep and 11,000 cattle were present within the English Nature countryside characteristic area of the Forest of Dean and Lower Wye. The rapid return of such large numbers of grazers, albeit about 50% less than the original levels, should have alleviated the original slaughter impact.

Another factor explaining the lack of impact of FMD on *Geotrupes* consumption is the number of bats actively foraging in winter. It is much lower than in summer. Summer bats forage from two to three times per night. Winter bats may forage from once every day to once every twelve days, according to their arousal frequency (Ransome 1971, Park and others. 2000). Furthermore, only bats lacking sufficient fat reserves, such as juveniles at the start of winter, and adult males in mid winter, normally need to forage in most winters (Ransome 1968, 2002). On a given night in summer, a population of 100 bats would carry out about 250 foraging bouts. A similar sized population in winter, consisting of 20% adult males and 20% surviving first-year bats, would carry out a maximum of 40 bouts per night at an arousal frequency of once a day, and 3.3 bouts at once in twelve days. These ranges represent between 16% and 1.3% of the summer level. Also, these calculations assume that all adult males and first-year bats forage at each arousal, and do so at the same time of winter. Neither is true, as is shown by the data from winter clusters presented above. About 45% of bats in clusters did not feed at their last arousal, even in mild winter weather. Hence the true levels may be about half of these figures, so competition for flying *Geotrupes* beetles among winter foraging bats may not be very high, even at hibernation sites containing quite large clusters.

8. Comparison of population parameters at Dean Hall and Woodchester Mansion before and after the slaughter

8.1 Introduction

Since the late 1980s studies have been carried out at the two roosts concurrently through the main summer period. They involved exit counts from the roost, counts and captures of the young born within the roost, and the collection of biometric data from the young. Hence the major data necessary to assess population performance were collected over many years prior to, and after FMD.

8.2 Methods

Both roosts were visited weekly and dusk exit counts were carried out to assess the numbers of bats present that had foraged and returned the previous dawn. After the count, the roost was entered to count and capture any young present. Each young was ringed and measured before being replaced within the roost prior to the return of their mothers. Forearm (radius) length was accurately measured (±0.2mm) using dial callipers, and also body mass using either digital scales or a 50g pesola spring balance (±0.1g). Young were aged to at least ±1 day of birth from either visual features (such as presence of an umbilical cord), or from past radius growth curves.

8.3 Results

8.3.1 Exit counts by year and site compared

The numbers of bats present in the maternity roosts were assessed by dusk exit counts on the nights that droppings were collected. Figures 14 and 16 summarise data for years 1997 to

2003. Data are only presented for weeks 3 to 11, as earlier weeks are highly erratic under the influence of climatic effects.

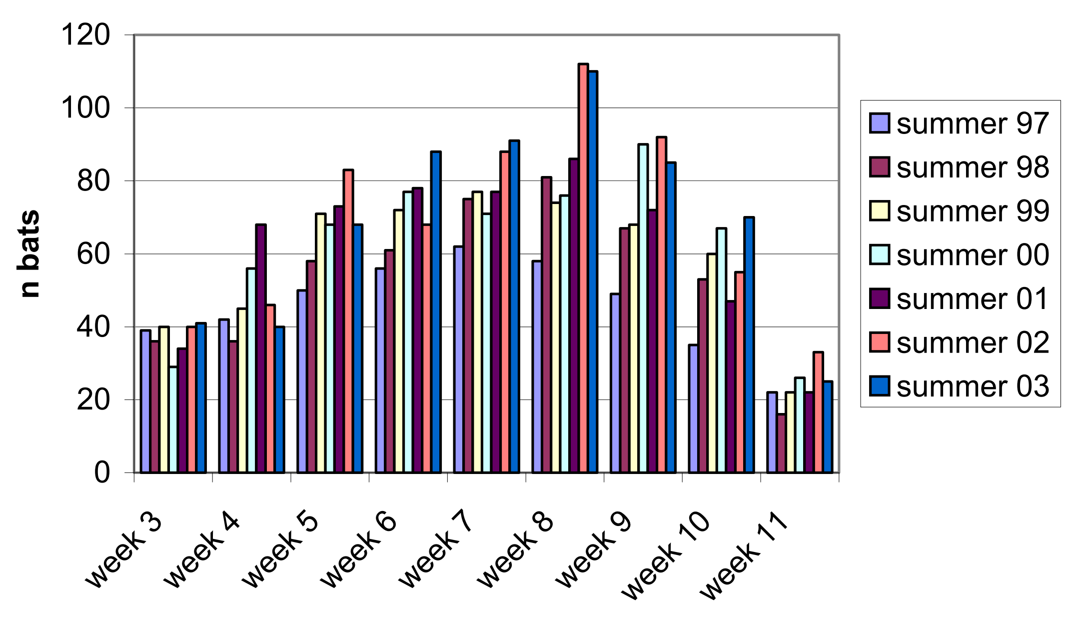

Figure 20 Woodchester exit counts by summer & week of the diet study

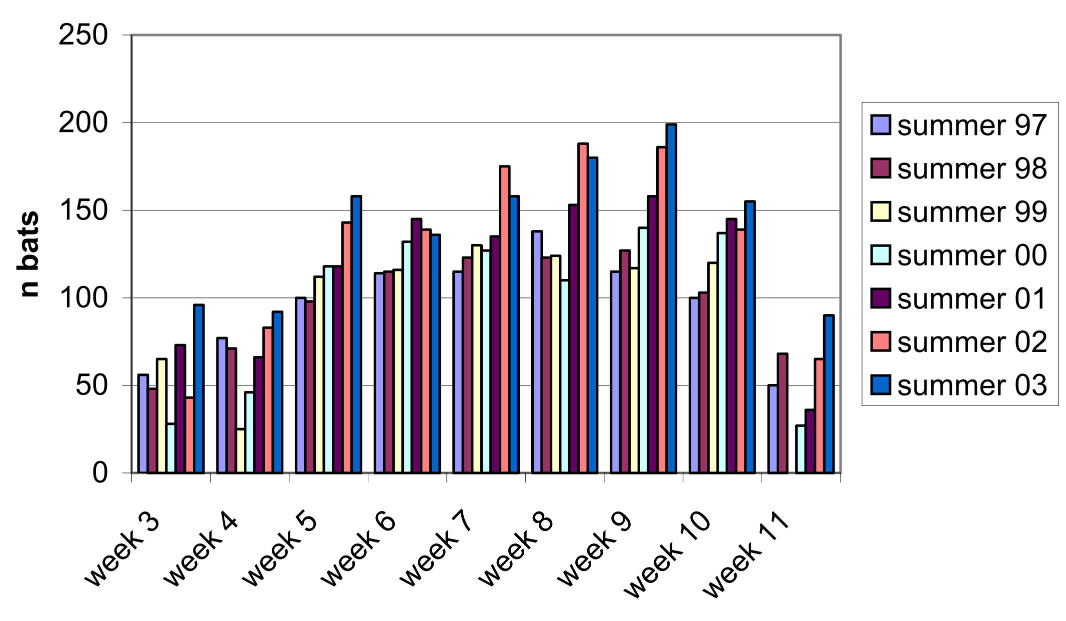

Figure 21 Dean Hall exit counts by summer & week of the diet study

The pattern of occupation is similar at the two roosts overall, but more bats remain at Dean Hall into early September (week 10) each summer. At both roosts from week 7 to 10 there is trend towards higher numbers with each year. No obvious impact of the slaughter can be seen from the raw data.

In order to examine the possible impact of the slaughter during the period when *Aphodius* consumption fell at both roosts, but particularly at Dean Hall, the data were converted into percentages. We predicted that the Woodchester data, as a percentage of Dean Hall should rise after FMD slaughter, then possibly fall again as restocking of grazers subsequently occurred from spring 2002. This prediction was based on the assumption that, in response to lower prey availability at Dean Hall, bats should disperse away from Dean Hall more than from Woodchester. Table 19 shows the results.

Table 19 Woodchester exit counts as a percentage of Dean Hall counts during weeks 7 to 11 from 1997 to 2003

Week of diet study	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**Mean %**
7	**53.9**	**61**	**59.2**	**55.9**	**57**	**50.3**	**57.6**	**56.4**
8	**42**	**65.9**	**59.7**	**69.1**	**56.2**	**59.6**	**61.1**	**59.1**
9	42.6	52.8	58.1	64.3	45.6	49.5	42.7	50.8
10	35	51.5	50	48.9	32.4	39.6	45.2	43.2
11	44	23.5	52.4	96.3	61.1	50.8	27.8	50.8
Mean%	**43.5**	**50.94**	**55.9**	**66.9**	**50.5**	**50**	**46.9**	**52.1**

Bold figures refer to the weeks when *Aphodius* consumption by juveniles is likely to critically affect the later stages of their growth.

The data shown did not support our prediction since the percentages fell markedly after 2000, when they peaked. Neither are there any obvious differences in the pattern of exit count numbers at the two roosts.

Discussion

The proportion of the colony that occupies the maternity roost through the summer fluctuates constantly (Ransome 1973, unpublished data for Woodchester by Peter Andrews and Roger Ransome). The reasons for these changes are poorly understood, but rapid changes over a few days seem to be related to sudden prey availability changes under the influence of weather. These are most likely to occur early and late in the summer.

Longer term changes may be linked to changes in insect phenology, that also alter prey availability, and to the requirement for female bats to congregate together when giving birth.

Exit count data show no obvious changes in the annual pattern of occupation by bats of the two roosts through the study period. Peak numbers still occurred during August after FMD, even during the period of *Aphodius* beetle deprivation. Bats still congregated within their respective roosts, enduring the consequences. This re-enforces other evidence for the strong attraction of the traditional roost to bats of this species.

8.3.2 Sex ratios by year and site compared

The sex ratio of birth cohorts at a maternity roost is an important population parameter. Female bats have single births, and usually about 95% of mature females breed annually (Ransome 1995). Hence the number of mature females largely determines annual birth numbers. Ransome (1998) showed that female births were linked with larger mothers, and warmer roosts (heated by incubators) improved growth rates resulting in larger female offspring. Hence incubators promote population recovery.

Table 20 summarises the birth sex data from summer 1997 to 2002 for the two roosts. Table 21 shows the results of chi-square tests carried out on the data over various time intervals.

Table 20 Sex of young born from 1997 to 2002 by site

YEAR(s)	WOODCHESTER			DEAN HALL		
	N females	N males	N total	N females	N males	N total
1997	15	15	30	17	22	39
1998	17	18	35	13	20	33
1999	23	16	39	23	13	36
2000	19	22	41	32	16	48
2001	27	19	46	23	26	49
2002	30	18	48	26	32	58
Totals	131	108	239	134	129	263
1997 & 1998	32	33	65	**30**	**42**	72
1999 & 2000	42	38	80	**55**	**29**	84
2001 & 2002	57	37	94	**49**	**58**	107

Grey background years are pre slaughter. Woodchester's roost had an incubator throughout these years; Dean Hall had an incubator installed in spring 1998. Bold figures show significant sex ratio changes through the paired years.

Table 21 Chi-square tests comparing sex ratios by years, FMD period and roost

Roosts and years compared	Degrees of freedom	Chi-square	P value	Significance
Woodchester 1997 to 2000	3	1.443	0.695	Not significant
Dean Hall 1997 to 2000	**3**	**9.053**	**0.029***	**Significant but no consistent trend**
Woodchester 2001 and 2002	1	0.142	0.706	Not significant
Dean Hall 2001 and 2002	1	0.048	0.827	Not significant
Woodchester pre and post FMD	1	0.027	0.869	Not significant
Dean Hall pre and post FMD	1	1.919	0.166	Not significant
Woodchester & Dean Hall pre FMD	1	0.359	0.549	Not significant
Woodchester & Dean Hall post FMD	**1**	**4.424**	**0.035**	**Significant – more males at Dean Hall**
Woodchester 1997 & 98 cf 1999 & 2000	1	0.153	0.695	Not significant
Woodchester 1999 & 2000 cf 2001 & 2002	1	1.167	0.280	Not significant
Dean Hall 1997 & 98 cf 1999 & 2000 (incubator effect)	**1**	**8.863**	**0.003**	**Highly significant; switch to females**
Dean Hall 1999 & 2000 cf 2001 & 2002 (FMD effect)	**1**	**7.350**	**0.007**	**Highly significant; switch to males**

Bold data are significant ($p < 0.05$) or highly significant ($p < 0.01$); cf = compared with.

Discussion

Sex ratios at Woodchester (table 20) were close to 1:1 pre FMD (74 females: 71males), and female births exceeded male births post FMD (57:37). This latter situation also occurred at

Dean Hall following the installation of an incubator in 1998. This event was followed by a significant swing towards female births in 1999 and 2000 (55:29). However, a trend towards male births at Dean Hall was seen in the two summers after FMD (49:58). As a result there was a significant difference between the sex ratios at the two roosts after FMD. A strong bias towards male-dominated births happened at two roosts in south-west Wales before a major population crash in the mid 1980s (Ransome & McOwat 1994). If maintained, the strong population recovery seen at Dean Hall in the late 1990s is likely to cease, and even turn into a decline.

8.3.3 Birth dates by year and site compared

Birth timing is an important factor influencing the growth and survival of young born within unheated roosts (Ransome 1989, 1998). Late-born young, and their mothers have an increased risk of mortality over the following year (Ransome 1995). The installation of an incubator within a roost to maintain it at about 27 °C improves both growth and survival rates (Ransome 1998 and subsequent unpublished data).

Pregnancy in UK bats lasts from April to June or July, and is interrupted by frequent bouts of torpor due to cold weather (Racey 1973). Ransome and McOwat (1994) showed that birth timing in greater horseshoe bats was synchronised at maternity roosts spread over a wide region by climatic temperatures in April and May. A mean temperature of 10 °C was necessary to result in a cohort mean birth date of 15 July. This effect results from the loss of foraging bouts, particularly at dawn, due to low temperatures preventing the flight of insect prey. Secondary prey in April, and *Melolontha* (cockchafers) in May, largely sustain pregnancy. Since neither of these food supplies would be directly affected by FMD slaughter, we predicted that birth timing would not be affected by FMD. It should only reflect climatic temperatures early in the summer.

We determined the birth dates of young born at the two roosts in the two years before and after FMD. The methods used are provided by Ransome and McOwat (1994). Table 22 summarises the data. Births were exceptionally early in 1999, early in 2002, and close to normal in the other years. These data reflected climatic conditions earlier in the summer.

Table 22 Birth dates at Woodchester and Dean Hall from 1999 to 2002

YEAR	WOODCHESTER			DEAN HALL		
	mean DBIRTH	N	St. Dev.	Mean DBIRTH	N	St. Dev.
1999	29.8	38	6.2	34.9	22	9.3
2000	41.3	40	6.1	40	31	5
2001	41.2	46	8.5	42.2	35	8.8
2002	34.6	47	5.9	37.5	35	7.6

DBIRTH = date of birth where June first = 1. Hence July first = 31.

Two-sample t tests were carried out on the combined data pre and post FMD slaughter, and for each year at the two roosts separately. Table 23 summarises the results.

Table 23 T tests comparing birth dates by FMD period and years and roost

Roost and years compared	Means	T-value	P value	Significance
Woodchester pre & post FMD	35.68 pre 37.86 post	-1.73	0.085	Not significant
Dean Hall pre & post FMD	37.85 pre 39.84 post	-1.38	0.169	Not significant
Woodchester & Dean Hall 1999	**29.72 Wd** **33.39 DH**	**-2.11**	**0.039**	**Significant**
Woodchester & Dean Hall 2000	41.28 Wd 40.65 DH	0.54	0.589	Not significant
Woodchester & Dean Hall 2001	41.28 Wd 42.12 DH	-0.46	0.646	Not significant
Woodchester & Dean Hall 2002	34.64 Wd 35.90 DH	-0.91	0.365	Not significant

Data for both sexes combined. **Bold** data are significantly different ($p< 0.05$).

Discussion

No trend in birth timing occurred over the four-year period. Only one year showed significant differences between the two roosts and that was in 1999, before the FMD outbreak. Hence, as predicted, FMD slaughter had no significant impact on birth timing.

9. Juvenile growth at Dean Hall and Woodchester Mansion before and after the slaughter

9.1 Introduction

Ransome (1998) showed that there were no sex differences between either the body mass or radius length of newly-born greater horseshoe bat young. Radius length change was the best judge of growth, since body condition varied considerably among individuals. Female young grew faster than males, and reached a larger ultimate size (mean 56.06mm compared with 55.05mm for males). Female growth was more affected by roost thermal conditions than that of the males.

Early growth rate during the period from age 4 to 14 days was the most important factor affecting final radius length (= forearm length). It explained about 45% of the variation in females, and 28% in males both before and after the installation of heaters. Body condition of the young during the early growth period explained about 10% of the variation in female forearm length both before and after heater installation. In unheated roosts, body condition explained about 15% of male forearm length, but none with heaters. Juvenile body condition reflects that of the mother on the day of capture (Duvergé and others 1999). These data are consistent with the hypothesis that mothers with poor body reserves, for whatever reason, are forced to reduce milk production and their young obtain less milk for both growth and storage. Because female young are more costly to rear, they are most vulnerable to milk deprivation.

Mothers may have poor body reserves for many possible reasons, but two are likely to be important ones. Firstly the absence of abundant food supplies, and secondly the high costs of maintenance during lactation in cool roosts. Ransome (1998) showed that female young grew significantly larger within a heated roost. (Forearm mean = 55.74mm unheated; 56.54mm with heaters; t_{71}= 3.41; p=0.0011.) This may seem to be a small change, but it was associated with a rise in female survival rate from about 40% to 60% and a switch to female dominated births as noted above. Subsequent data has shown that the improved survival rate is significant (Ransome, unpublished data).

Hence, if FMD slaughter reduced *Aphodius* food supplies to lactating female bats, it is predicted that the final stages of growth, when these beetles are eaten, and survival of female young are likely to be affected.

9.2 Methods

Juvenile bats were caught after the exit of the adults at both roosts. All were ringed and measured accurately (Ransome 1998). At Woodchester visits were made twice a week, with assistants, to obtain growth curves for individuals that were subsequently captured with adults at monthly intervals to October. Hence the body condition, early survival and forearm growth achieved was known in detail.

At Dean Hall visits to capture the young were made once a week after births started, and ceased once they were volant. DJP had problems obtaining help to process the young in some summers, and so did not obtain weight data for all of them. Consequently early survival of individuals could not be followed, and full condition data was not available to the study. The final radius achieved by cohorts was obtained by measurement after the capture of ringed first year bats within nearby hibernacula in mid winter.

Complete body condition for the summers of 1997 to 2003 were only available for Woodchester bats. Since the dietary impact of FMD slaughter in summer was only discernable from week 7 (late July), two periods were selected. One was 20 July in each year (plus or minus one day), when most juveniles are sustained by milk from their mothers that normally feed on moths at that time of the summer. The other period was 27 July combined with 3 August (plus or minus one day for each date). This period will be called the late July period. The first period was just prior to the emergence of adult *Aphodius* beetles, and the second included the early days of emergence when juvenile bats would be starting to forage (Duvergé and others 1995). Only female juveniles were studied, since male growth and survival is unaffected by condition in heated roosts (Ransome 1998).

We predicted that on 20 July each summer, since moth consumption was not affected by FMD, condition levels should be similar throughout the seven summers.

We further predicted that, as *Aphodius* consumption was high at both roosts prior to FMD, and it fell at both roosts afterwards, body condition in late July should fall at both sites in late July from 2001.

As body condition data for Dean Hall were only complete for the three summers after FMD, t tests to compare data for these years between the two roosts were first carried out. They established that there were no significant differences between them during late July (t_{101} = 1.40; p = 0.165; NS). Data for the two roosts were therefore combined to assess the impact of FMD through the seven-year span.

9.3 Results

Table 24 shows female forearm growth data at the two roosts for two years prior to FMD and two years afterwards.

Table 24 Final forearm lengths of female cohorts by year of birth and site

BIRTHYEAR	WOODCHESTER			DEAN HALL		
	mean FFL (mm)	N	St. Dev.	mean FFL (mm)	N	St. Dev.
1999	56.32	21	1.03	55.84	14	0.94
2000	56.41	15	1.65	56.40	19	1.11
2001	56.38	24	1.18	56.49	17	0.71
2002	**56.70**	**21**	**0.91**	**55.69**	**13**	**1.19**

Shaded rows are pre FMD; unshaded rows are post FMD. Bold data are significantly different.

Mean data show remarkable similarity between the roosts for the summers of 2000 and 2001. In 1999 and 2002 Dean Hall females grew less than those at Woodchester.

Table 25 shows the results of T tests carried out on the data in table 23.

Table 25 T tests comparing female forearm lengths by years and roost

Roost and years compared	**Means (mm)**	**T-value**	**P value**	**Significance**
Woodchester pre & post FMD	56.36 pre 56.53 post	-0.62	0.534	Not significant
Dean Hall pre & post FMD	56.16 pre 56.15 post	0.06	0.984	Not significant
Woodchester & Dean Hall 1999	56.32 Wd 55.84 DH	1.40	0.171	Not significant
Woodchester & Dean Hall 2000	56.41 Wd 56.40 DH	0.03	0.978	Not significant
Woodchester & Dean Hall 2001	56.38 Wd 56.49 DH	-0.35	0.731	Not significant
Woodchester & Dean Hall 2002	**56.70 Wd** **55.69 DH**	**2.78**	**0.009**	**Significant**

Bold data are significantly different ($P < 0.01$).

Only the differences for 2002 were statistically significant, with Dean Hall female young showing smaller forearms. In 1999, although Dean Hall bats were smaller, data were not significant. That summer at Dean Hall a group of female mothers gave birth to female offspring late in the season, significantly lowering the birth date that year in comparison to Woodchester (see table 25). This situation may have been due to first-time breeders that are known to give birth much later than experienced mothers (Ransome 1995).

Table 25 shows the results of a one-way analysis of variance of body condition data, combined for the two roosts, for the 20 July from 1997 to 2003. Data are shown graphically in figure 22.

Table 26 One-way Anova of female body condition on 20 July versus year (combined data for the two roosts)

Source	**DF**	**SS**	**MS**	**F**	**P**
Year	6	3.942	0.657	0.94	0.471 NS
Error	160	112.317	0.702		
Total	166	116.260			
Level	**N**	**Mean**	**St. Dev.**		
1997	19	15.274	0.639		
1998	12	15.142	0.821		
1999	11	15.127	1.074		
2000	24	15.167	0.651		
2001	35	15.057	0.804		
2002	29	15.483	0.979		
2003	37	15.059	0.874		

Mean data are in g. Lethal limit for juveniles is about 12.5g. Serious growth problems develop increasingly below 14.5g.

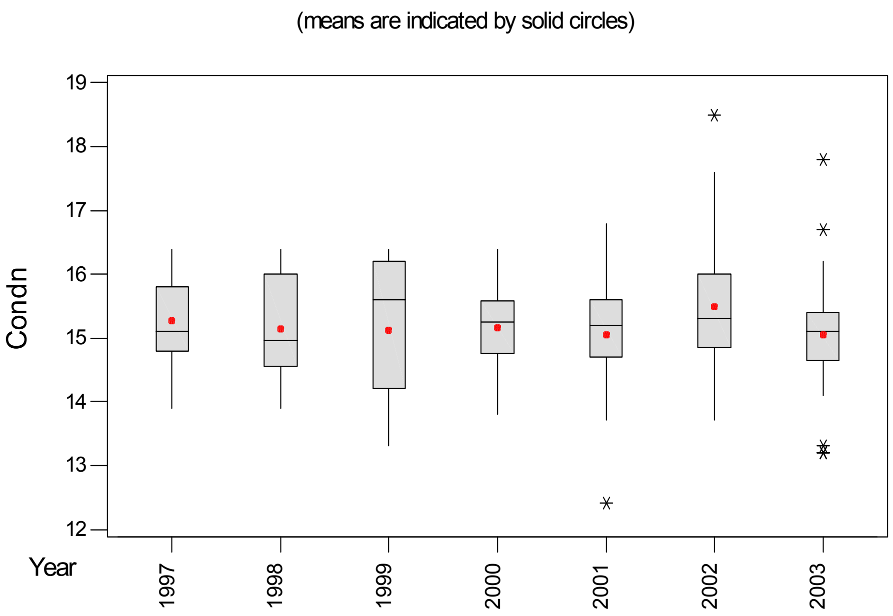

Figure 22 Condition of female juveniles on 20 July by year

No significant differences in female body condition existed for any of these summers. In 2002 the mean of 15.48g was the highest recorded.

Table 27 shows the results of a one-way analysis of variance of body condition data, combined for the two roosts, for late July from 1997 to 2003. Data are shown graphically in figure 23 by year, and combined as pre and post FMD data in Figure 24.

Table 27 One-way Anova of female body condition in late July versus year (combined data for the two roosts)

Source	**DF**	**SS**	**MS**	**F**	**P**
Year	6	84.49	14.08	13.75	0.000
Error	172	176.13	1.02		
Total	178	260.62			
Level	**N**	**Mean**	**St. Dev.**		
1997	19	15.716	0.911		
1998	18	15.383	0.934		
1999	25	16.428	1.715		
2000	27	15.056	0.962		
2001	29	14.697	0.811		
2002	15	14.707	0.581		
2003	46	14.367	0.796		

Mean data are in g. Lethal limit for juveniles is about 12.5g. Serious growth problems develop increasingly below 14.5g.

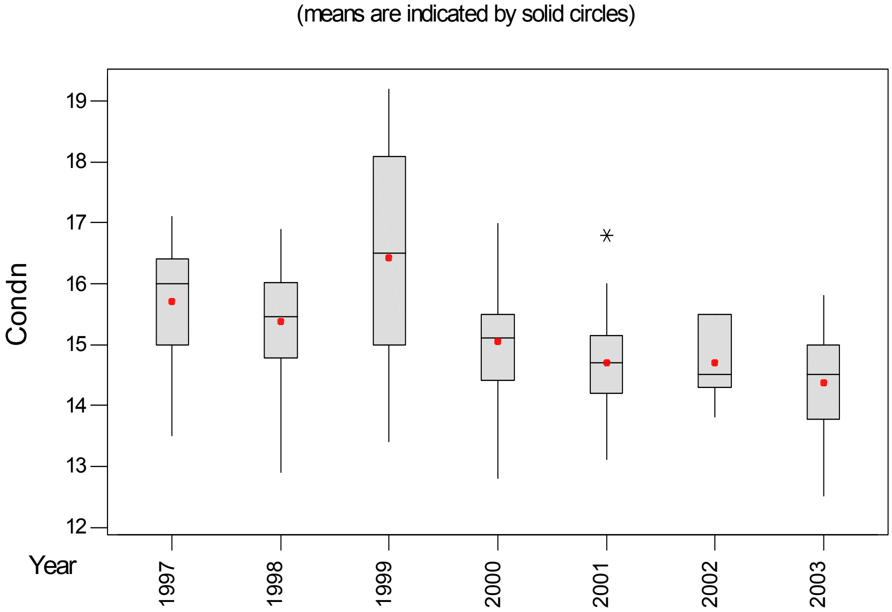

Figure 23 Condition of juvenile females in late July by year

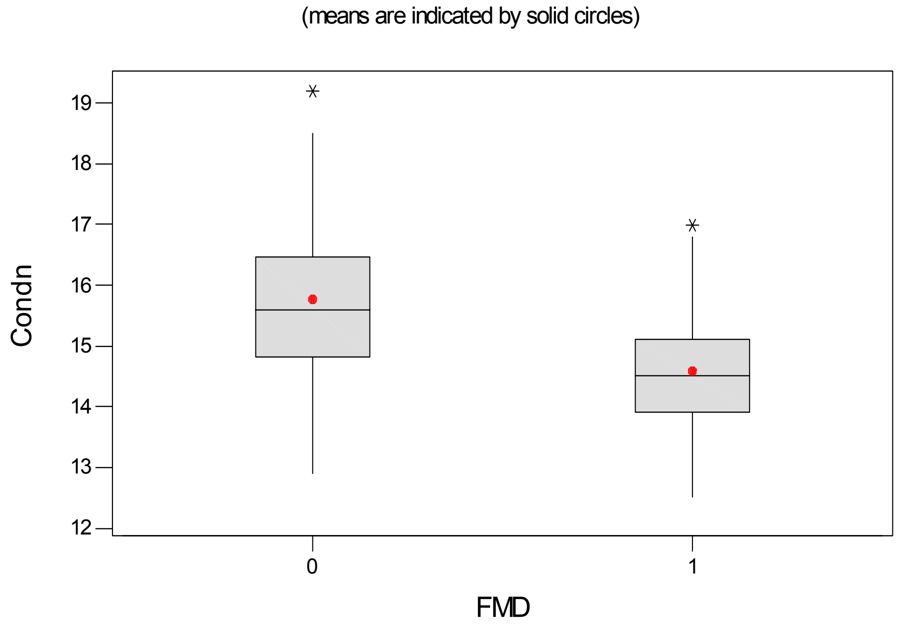

Figure 24 Condition of female juveniles in late July before and after FMD

The Anova analysis shows that significant differences in female body condition existed for some of these summers. In 1999 the mean of 15.48g was the highest recorded. In later summers the levels progressively fell, reaching the lowest level in 2003 of 14.37g.

9.4 Discussion

Smaller forearm length in female bats indicates general growth stress (Ransome 1998). Since all female young born at the two roosts in 2002 were born within incubators, thermal stress cannot be a cause of the significant growth differences seen at the two roosts that summer. Lactating bats at Dean Hall consumed much lower amounts of insects in 2002 than those at Woodchester (table 7), and are predicted to have reduced milk supplies to their young once their body reserves became critical.

As predicted, we found no significant differences in the female juvenile body condition of bats on 20 July (table 26). However, over the next two weeks, condition fell significantly after FMD slaughter (table 27), supporting the view held by Speakman and Racey (1987), that lactating bats have only enough body reserves to sustain themselves for a few days. Since the mean levels in late July were below 14.5g, many bats were well below this figure. They must have experienced growth rate reductions that would have lead to stunting. This is confirmed by data at Dean Hall presented in table 25 in 2002. Four young either starved to death or their mothers aborted them within the roost. Others may have starved during their early foraging flights.

10. Female juvenile survival at Woodchester Mansion before and through the slaughter period

10.1 Introduction

A series of severe winters and late cold springs results in late birth dates and a switch to male-dominated births (Ransome & McOwat 1994). A major climate-induced population crash of greater horseshoe bats occurred throughout the UK, following the exceptionally cold spring of 1986. Ransome (1989) documented this change for sites near Bristol, and suggested a mechanism to account for it. Late-born bats, especially females, were growth-stunted and had poor survival prospects.

At Woodchester the number of live births fell from 50 to 60 in the early 1980's, and to 19 in the summer of 1987. Six years later, the numbers of births had only risen to 24. In the summer of 1994 an incubator system was used to heat the breeding attic. Several years later, English Nature arranged cattle-grazing improvements within the Woodchester valley, in an attempt to promote population recovery. By the summer of 1997 live births had risen to 30. Furthermore, as time went on, births sex ratios were either equal, or female dominated, as shown above. Female growth improved (Ransome 1998), and survival rates rose from about 40% to over 60% as discussed in part 9. These data, however, give only a partial insight into the performance of a population. Greater horseshoe bats show delayed sexual maturity, with some females breeding at age 2 years, and others at 3 or older. Individuals may live for 30 years, but there is a trade-off between number of young born and the length of survival (Ransome 1995). What really matters is how many females reach reproductive age, the sex ratio of their offspring, and their long-term reproductive potential.

Rises in female survival rates at Woodchester may have been due to the improved roost thermal regimes, better foraging conditions within the valley, or a combination of both. This part reviews evidence for an impact on the survival and future reproductive potential of female cohorts born from 1995 to 2002. We predicted that the reduced *Aphodius* beetle availability would increase juvenile mortality at weaning, and possibly survival to breeding age over the longer term. As Woodchester was less affected by FMD slaughter than Dean Hall, any impacts noted there were likely to have been more severe at Dean Hall.

10.2 Methods

The methods used to obtain survival data are fully explained in Ransome (1995). Essentially females return annually each summer to breed at their natal roost. Although they show occasional years of non-breeding, females still return for short periods. Since captures of the whole colony were monthly from May to October, live bats are rarely missed.

10.3 Results

Table 28 summarises the data obtained to date.

Table 28 Survival of female bats year of birth to breeding age for cohorts born 1995 to 2002

Year of birth	N females born (total births)	N alive 1 year later (%)	N breeding early (2 years)	N breeding late (3+ years)	Total reaching breeding age (%)
1995	16 (29)	8 (50%)	3	2	5 (31%)
1996	15 (32)	11 (73%)	7	2	9 (60%)
1997	15 (30)	11 (73%)	7	3	10 (67%)
1998	15 (33)	11 (73%)	5	5	9 (60%)
1999	23 (39)	15 (65%)	8	2	10 (44%)
2000	19 (41)	9 (47%)	2	2	4 (21%)
2001	27 (46)	11 (41%)	5	?	?
2002	29 (47)	11 (38%)	?	?	?

Source (Ransome unpublished data). Percentages are calculated from the numbers of births. ? means data not yet obtained.

The number of surviving females one year after birth remained remarkably constant. In 1995 a severe drought affected much of southern England and Wales from late June, delaying *Aphodius* emergence until early September (Ransome 1996). Table 28 shows that the 1995 drought impact upon female cohort survival was as severe as that of FMD later on. The percentage surviving from 1995, and those reaching breeding age, were both akin to the post FMD period, and therefore 1995 data were not used in chi-square tests in the pre FMD period shown in table 29 below.

From 1996 to 2002 survival was very high, then began to decrease in recent years to the lowest in 2002. The number and percentage reaching reproductive age also shows a similar pattern. Unfortunately data for survival to breeding age from the 2001 and 2002 cohorts will not be available for some years. However, by making a few assumptions about survival rates we can estimate the likely numbers reaching breeding age.

Of the 45 female bats that were born in the pre FMD (1996 to 1998) unaffected years, 28 (62%) reached breeding age. Of the 42 female bats that were born in 1999 and 2000, and were exposed to FMD effects before breeding, 14 (33%) reached breeding age. The survival to breeding age of females born in 2001 and 2002 seems likely to fall still further, since fewer of them survived to one year old (table 28). Hence calculations were made using the two percentages to estimate the numbers of females surviving to reproductive age. They were 33%, on the assumption that the FMD effects would remain the same, and 20% on the assumption that FMD had already lowered the numbers reaching age one, and would be compounded later on. These numbers were then used in chi-square tests on the numbers born and those surviving to breeding age for the two periods. Results are shown in table 29.

Table 29 Chi-square tests comparing estimated Woodchester female cohort survival to breeding age by periods affected by FMD

Assumption made for calculations applied to 2001 & 2002 births	N calculated to reach breeding age from 2001 & 2002 cohorts	Chi-square	P value	Significance
33% survival of female cohorts to breeding age	**19**	**3.876**	**0.049**	**Significant**
20% survival of female cohorts to breeding age	**11**	**7.549**	**0.006**	**Highly significant**

Years unaffected by FMD were compared with those that were affected: combined years: 1996 to 1998 compared with 1999 to 2002. All with DF = 1. Remaining data extracted from table 28. See text for a full explanation.

10.4 Discussion

A female bat born in 1997 would have become an early breeder in 1999, or a late breeder in 2000. It would be unaffected by FMD slaughter until either its second or third parturition. Female bats have an increased risk of dying after their first parturition, possibly due to giving birth very late in July (Ransome 1995). This is especially true of early breeders. Females born in 1997 would not have been exposed to any additional mortality risks at this time due to FMD impacts. In contrast, female bats born in 1999 would have given birth in 2001 if they were early breeders, and 2002 as late breeders. Both parturition years would have been affected by FMD slaughter impacts.

Table 28 shows that the survival rate of the 1997 Woodchester cohort was 73% to one year, and 67% to first parturition. Conversely the 1999 cohort's equivalent data were 65% and 44% respectively. The largest difference was in survival to breeding age.

Female bats born in 2000, the summer before FMD, showed markedly reduced survival rate over their first year to 47%. This increased mortality happened before *Aphodius* reduction in the colony diet occurred, so cannot be attributed to FMD. However, this cohort would have been exposed to any FMD impacts by the time they became breeders. Their overall survival rate to first-time breeding was the lowest at 21%. The estimated survival of female bats born in 2001 and 2002 shown in table 29, indicate that these changes are either statistically significant, or highly significant.

The data in table 28 can be interpreted as being consistent with the predicted adverse impact of FMD upon bats, via reduced food supplies, lower survival and reproductive success. It can also be interpreted as being due to the Woodchester colony reaching the carrying capacity of its surrounding foraging habitat, within its foraging commuting range (Ransome 1996). However, in the early 1980's the colony consisted of a total population of some 180 bats, 130 of which flew out of the Mansion through mid summer, and 50 to 60 births annually. In 2003 there were 50 births, and a peak of 88 adults in early July. The maximum exit count was 108 bats. As the population had benefited from an incubator to raise roost temperatures in 1994, and enhanced foraging regimes since then, the former hypothesis is more likely to be correct. Further support for this view comes from survival data for the1995 female cohort. At a period when the number of births was only 29, similar survival to one year and breeding age occurred as in the years exposed to FMD effects. The deprivation of *Aphodius* beetles from late-lactating adults and their foraging young was the common factor.

At Dean Hall the number of births has shown a similar rising pattern, slightly ahead of Woodchester (table 20), but with much higher numbers of non-breeding bats. The population there seems likely to suffer at least the same level of increased mortality. If so, then the population recovery seen at both roosts is predicted to terminate very soon in the absence of a recovery in *Aphodius* availability.

11. Synthesis of diet, population and growth data differences before and after the slaughter

11.1 Summer diet changes in relation to the slaughter

The insect prey consumed by greater horseshoe bats at Woodchester Mansion and Dean Hall in the summers of 1996 and 1997 were virtually the same. In the summer of 1998 Woodchester bats ate more *Aphodius* beetles, and Dean Hall bats ate more moths. Both insects are key prey, and the differences in 1998 may have related to either the absence of cattle close to Dean Hall that summer, or much greater supplies of moths within the Forest of Dean, than near Woodchester Mansion.

In the summer of 2001, immediately after FMD slaughter, a total of four prey items were consumed at significantly different levels at the two sites. These differences only affected insects consumed from late July to early October. At this time *Aphodius* consumption was significantly higher at Woodchester than at Dean Hall. However, consumption fell at both roosts, but did so more severely at Dean Hall. Moth consumption was significantly higher at Dean Hall. Hence the key prey differences noted in 1998 were repeated, but levels of *Aphodius* consumption fell to low levels at both roosts. Bats compensated partly for their reduced key prey intake by switching to two kinds of secondary prey. At Woodchester they ate significantly more summer chafers than did bats at Dean Hall. Bats at Dean Hall ate significantly more tipulids than those at Woodchester.

In the summer of 2002, the second summer after FMD slaughter, three prey items were consumed at significantly different levels at the two sites. The differences also only related to the late July to early October period, but they increased to highly significant levels in each case. As in 2001, Woodchester bats ate more *Aphodius* beetles, and Dean Hall bats more moths and tipulids. However, amounts of *Aphodius* beetles consumed rose at both sites, possibly reflecting the restocking of some grazers in spring 2002, and/or the expansion of deer populations that were not slaughtered.

Changes in prey consumption after FMD slaughter at the two roosts were not entirely as predicted. The reduced *Aphodius* levels at Dean Hall were expected, but those at Woodchester were not. The data provided by this study suggest that dung beetles are locally concentrated by grazers that need to be kept very close to roosts from mid July through October. The adult beetles can fly long distances (at least 10km) from their population sources. Prior to FMD slaughter, Woodchester bats benefited from cattle grazing very close to the Mansion, and large surrounding populations of beetles, some of which may have derived from the Forest of Dean. After FMD, although the cattle were still grazed close to the Mansion at similar levels, the lower levels of distant populations because of the slaughter may have been the cause of reduced consumption.

Amounts of summer prey consumed per bat per day were estimated from dry dropping production by each colony, and dusk exit counts. Data were calculated as mean dry droppings per bat per day, or F (in mg), for three weeks during the lactation period in three different summers. They were 1997, 2001 and 2002. At Woodchester, F levels fell from 581 in 1997 to 556 in 2001, and 514 in 2002. This represents an 11.5% fall through the period. No increase in juvenile mortality within the roost was noted. At Dean Hall F levels fell from 429 in 1997 to 378 in 2001, and 294 in 2002. This represents a 31.5% fall through the same period. Juvenile mortality within the roost increased, especially in 2001.

11.2 Winter diet changes in relation to the slaughter

Winter diets were investigated at both roosts through the winters (October to April) of 2001/2 and 2002/3 after FMD slaughter. At Woodchester comparisons with pre FMD winters was possible, using material previously collected and analysed. The amounts of dry droppings collected at Woodchester increased from winter 1997/8 to 2000/1, and levelled off in winters 2001/2 and 2002/3. Diet content at Woodchester was similar before and after FMD, showing low *Geotrupes* dung beetle and high *Ophion* wasp levels. At Dean Hall only post FMD data were available. Amounts of dry droppings collected were much greater than at Woodchester, especially in October and November. The diet quality at Dean Hall was superior to that at Woodchester, especially in 2002/3, with about 50% *Geotrupes* beetles being eaten.

Winter diets at two hibernation sites were also investigated by the capture of torpid bats. They were bagged up individually to collect droppings from known (ringed) individuals. The amounts of droppings per bat, and their specific diet prior to capture were determined. Bats at Cinderford were captured in early December in 1998, 1999, 2001 and 2002. Bats at Symonds Yat were captured in mid February in 1999, 2002 and 2003. At both hibernacula were located within the Forest of Dean FMD slaughter area. Neither the amounts of prey consumed, nor the diet content showed any deterioration over the two winters after FMD slaughter. *Geotrupes* consumption remained very high (over 90%) at both sites. These data were not predicted. Possibly the feral deer populations in the Forest of Dean, and the restocking that occurred from spring 2002, were sufficient to maintain *Geotrupes* levels that were profitable to these bats.

The dispersal of bats to other sites from the major hibernaculum near Cinderford, seems to have been the result of lower *Geotrupes* populations in the second winter after FMD slaughter. This, and the historical data from Minchinhampton Common and mines, suggests that bats may visit hibernacula to assess their foraging potential prior to the onset of hibernation, possibly in September, when many older bats leave the maternity roosts.

11.3 Population changes related to the slaughter

Three parameters that indicate or can potentially affect population levels were assessed through the pre and post FMD period. Dusk exit counts were carried out through the summers of 1997 to 2003. Also the sex ratios (1997 to 2002) and birth dates (1999 to 2002) of the juveniles born were monitored. Exit counts at both roosts continued to rise strongly through these years with a possible levelling off in 2003. Sex ratios of juveniles born showed no significant differences between the pre and post FMD period using combined data for the two roosts, and in the pre FMD period there were no sex ratio differences between the two roosts. At both roosts more females were born than males. However, in the post FMD period sex ratios were significantly different at the two roosts, with more females born at

Woodchester and more males at Dean Hall. The trend towards male births seen at Dean Hall after FMD is indicative of diet or climate stressed populations. It is likely that the deterioration in both the quality and quantity of prey eaten at Dean Hall following FMD slaughter was responsible.

Birth dates showed no trend between 1999 and 2002, and data for the two roosts were not significantly different from 2000 to 2002. In 1999 Woodchester bats were born significantly earlier than Dean Hall bats, but as this was before FMD, the slaughter cannot have had any impact. Pre and post FMD data from the two roosts separately showed slightly later births after FMD, but the differences were not significant.

11.4 Juvenile birth and growth changes related to the slaughter

The growth of the forearms of female juveniles at the two roosts from 1999 to 2002 was studied, using two slightly different methods. At Woodchester all surviving juveniles were regularly captured from birth to weaning and full size by late August. Consequently data were available for all females. At Dean Hall juveniles were ringed at about 10 to 14 days old, and only recaptured within the hibernation site at Cinderford in the following December. Consequently if smaller females died prior to reaching the hibernation site, the sample would have been biased in comparison with the Woodchester data.

Female forearm growth, as assessed above, showed no significant differences between the pre and post FMD data for either Woodchester or Dean Hall colonies. Furthermore, over the four summers, only in 2002 did significant differences show up between the roosts. Dean Hall bats were smaller than Woodchester bats.

Body condition of female juveniles was also assessed at the two roosts at two periods of the summers from 1997 to 2003. As data from Dean Hall were sparse, no comparisons between the two roosts were possible, so data were combined. On 20 July, at a time when lactating females would not have been eating dung-dependent prey, there were no significant differences among these years, and mean data were well above starvation levels. By late July (between 27 July and 3 August) when dung dependent prey (especially *Aphodius* beetles), would normally have been a major part of the diet, condition levels were high before FMD, and significantly lower in the three summers after FMD. Many bats were very close to starvation levels.

Body condition of female juvenile bats did not deteriorate until late in their growth period, probably in response to reduced *Aphodius* beetle consumption. Hence forearm growth of most juveniles would have largely been complete before they and their mothers became seriously diet stressed. This may explain the failure to show the impact of FMD upon mean female forearm length in 2001.

11.5 Survival of female cohorts at Woodchester

Female juvenile cohorts born at Woodchester from 1996 to 2002 showed a steep decline in survival rates from 73% for 1996 to 1998, down to 38% for 2002. Similarly, and perhaps more importantly, survival to breeding age fell from about 62% from 1996 to 1998, to 44% in 1999 and 21% in 2000. These declines were not quite statistically significant due to the small numbers born each summer. Similar data were not available for Dean Hall cohorts as bats were not captured. However, since the FMD slaughter diet impacts were more severe at

Dean Hall, and roost mortality was higher, it is very likely that survival rates there were even lower. These figures must translate into a halt in the encouraging population increases at both roosts through the 1990s, unless foraging conditions improve significantly and rapidly.

11.6 Summary of slaughter impacts on bats

The following hypothesis accounts for the findings listed above.

FMD slaughter had a major impact on the populations of *Aphodius* dung beetles flying within the Forest of Dean from late July to October 2001, reducing them substantially. At Dean Hall, the absence of grazers close to the roost, resulted in very low availability of these beetles as food for both lactating females and their young in late July, since they normally concentrate near cattle providing fresh dung. At Woodchester, which was outside the slaughter area, and where cattle were kept close to the roost throughout the study, *Aphodius* consumption fell as well. This is thought to be the result of lower beetle populations over a wide area, including parts of the Forest of Dean, from which these insects may be drawn.

FMD slaughter had no impact upon birth dates at either roost, since the diet of bats during pregnancy involves few dung-dependent insects. Similarly, early lactation and growth of the young were not affected, as bats fed mainly on moths. In late July, towards the end of lactation and during the early juvenile foraging flight period, the poor supplies of *Aphodius* became a critical factor. At both roosts, as moth supplies fell, bats were forced to switch to secondary prey that did not sustain normal body condition levels. Juvenile growth completion was seriously harmed, especially at Dean Hall, where some juveniles starved in late July and early August. Mortality rates over the bat's first year, and to first breeding, are known to have risen at Woodchester. Similar data are not available for Dean Hall. Any increase in mortality rates there over the year after birth is unlikely to be due to over-wintering factors, since *Geotrupes* dung beetle consumption in both December and February remained high at Forest of Dean hibernacula, and the winters since FMD have been mild. Reduced *Geotrupes* populations in the winter of 2002/3 resulted in bats dispersing away from their Cinderford hibernaculum to other sites, including the Nailsworth mines where foraging conditions seem to have been temporarily superior.

12. Recommendations for grazing regimes near bat roosts

This English Nature Research Report required an assessment of any long-term threat to the maternity sites and, if appropriate, make recommendations for priority areas to restore grazing.

To mitigate against the damage we have shown has been caused by FMD slaughter, we recommend for all roosts within and adjacent to FMD outbreak areas:

1. that the environmental prescriptions made by Ransome (1996, 1997a) continue to be vigorously implemented, since this study reinforces their value. Deciduous woodland strips, adjacent to permanently-grazed pastures close to roosts, provide ideal conditions. It is especially important for significant numbers of cattle to be grazed as close to roosts as possible from mid July until at least late August, and preferably to mid October.

2. Habitat structure for foraging bats should be of the highest quality within the young sustenance zone, up to 1 km from each roost, and especially within 0.5km. This measure will ensure that *Aphodius* beetles will be concentrated just outside roosts, when juveniles first start to forage, since they many are drawn from larger populations further away.

3. In order to sustain large populations of *Aphodius* beetles in the surrounding areas, land managers should be encouraged, by appropriate support measures, to maintain grazers at distances up to at least 10km from the roost. This is the minimum distance that these beetles have been shown to fly to fresh dung. Furthermore this range is likely to contain many important hibernacula that will also benefit from grazers.

4. The grazers may be cattle, sheep, horses or deer, and they should be kept at sustainable densities that allow them to be kept outside on pastures throughout the year. Cattle grazing is preferred in summer, but can be followed by sheep or horses in winter. This is a good combination that helps to reduce the impact of parasites upon the health of the grazers, and minimises the need for potentially treatments that could harm the ecosystem (Ransome 1996). Sheep grazing adjacent to woodland from October to May is especially recommended, as sheep maintain a short sward that favours large populations of cockchafers and tipulids.

5. Habitat structure should also be of high quality within the roost sustenance zone at distances between 1km and 3 km from the maternity roost, or at greater distances if radio-tracking studies have shown them to be important, for summer foraging.

6. Further away, up to at least 10km from the roost, grazers of all kinds should be encouraged provided they are kept out in fields, and arable/urban sprawl discouraged. The habitat structure for foraging greater horseshoe bats is likely to be less important beyond 3km, unless previously shown otherwise by radio-tracking studies. Grazers at distances between 3 and 10km may be kept under a variety of habitat conditions around most roosts. They will still be beneficial in comparison with arable or urban areas, whatever their habitat structure, provided grazers are kept on permanent pastures. Deciduous forest with numerous grassy glades is most preferred, followed by parkland and orchards, with open fields delimited by barbed wire fences the least preferred option.

7. Habitat structure should also be of the highest quality near important hibernacula, where bats are most likely to need to forage in winter. Cattle and/or sheep and/or horses should be grazed within 1km, and preferable within 0.5km, of their entrances from early September through to the following April. They should be kept at sustainable densities that do not cause excessive poaching of the pastures. Where cattle and/or horses would cause serious poaching, sheep should be used.

13. References

DUVERGÉ, P.L. 1997. *Foraging activity, habitat use, development of juveniles, and diet of the greater horseshoe bat (*Rhinolophus ferrumequinum *- Schreber 1774) in south-west England.* Unpublished Ph.D. Thesis. University of Bristol.

DUVERGÉ, P.L. and others. 1999. Functional significance of emergence timing in bats. *Ecography,* 23, 32-40.

JONES, G. 1990. Prey selection by the greater horseshoe bat *Rhinolophus ferrumequinum*: optimal foraging by echolocation? Journal of Animal Ecology, 59, 587-602.

JONES, G., & RAYNER, J.M.V. 1989. Foraging behaviour and echolocation of wild horseshoe bats *Rhinolophus ferrumequinum* and *R. hipposideros* (Chiroptera, Rhinolophidae). *Behavioural Ecology and Sociobiology*, 25, 183-191.

JONES, G., DUVERGÉ, P.L., & RANSOME, R.D. 1995. Conservation biology of an endangered species: field studies of greater horseshoe bats. *Symposium of the Zoological Society of London*, 67, 309-324.

KONSTANTINOV, A.I. 1989. The ontogeny of echolocation functions in horseshoe bats. *In*: V. HANÁK, I. HORÁCEK & J. GAISLER, eds. *European bat research 1987*, 271–280. Praha: Charles University.

KUNZ, T.H. 1974. Feeding ecology of a temperate insectiviorous bat *Myotis velifer*. *Ecology*, 55, 693-711.

LANDIN, B-O. 1961. Ecological studies on dung-beetles (Col. Scarabaeidae). *Opusc. Ent. Suppl.* **XIX. -** Lund.

LANDIN, B-O. 1968. The diel flight activity of dung-beetles (Col. Scarabaeidae). *Opusc. Ent. Suppl.* **XXXIII.** – Lund.

PARK, K.J., JONES, G., & RANSOME, R.D. 1999. Winter activity of a population of greater horseshoe bats *Rhinolophus ferrumequinum. J. Zool. Lond.,* 248, 419-427.

PARK, K.J., JONES, G., & RANSOME, R.D. 2000. Torpor, arousal and activity of hibernating Greater Horseshoe Bats *Rhinolophus ferrumequinum. Functional Ecology,* 14, 580-588.

RACEY, P.A. 1973. Environmental factors influencing the length of gestation in heterothermic bats. *Journal of Reproduction and Fertility Supplement,* 19, 175-189.

RANSOME, R.D. 1968. The distribution of the greater horseshoe bat, *Rhinolophus ferrumequinum*, during hibernation, in relation to environmental factors. *Journal of Zoology, London*, 154, 77-112.

RANSOME R.D. 1971. The effect of ambient temperature on the arousal frequency of the hibernating greater horseshoe bat *Rhinolophus ferrumequinum*, in relation to site selection and the hibernation state. *Journal of Zoology, London*, 164**,** 357-371.

RANSOME, R.D. 1973. Factors affecting the timing of births of the greater horseshoe bat *Rhinolophus ferrumequinum*. *Periodicum Biologorum*, 75, 169-175.

RANSOME, R.D. 1978. Daily activity patterns of the greater horseshoe bat *Rhinolophus ferrumequinum*, from April to September. *In*: R.J. OLEMBO, J.B. CASTELINO, & F.A. MUTERE, eds. *Proceedings of the Fourth International Bat Research Conference,* 259-274. Nairobi: Kenya Academy for Advancement of Arts and Science, Kenya Literature Bureau.

RANSOME, R.D. 1989. Population changes of greater horseshoe bats studied near Bristol over the past twenty-six years. *Biological Journal of the Linnean Society*, 38, 71-82.

RANSOME, R.D. 1991. Greater horseshoe bat. *In*: G.B. CORBET & S. HARRIS, eds. *The handbook of British mammals*, 88-94. Oxford: Blackwell.

RANSOME, R.D. 1995. Earlier breeding shortens life in female greater horseshoe bats, *Philosophical Transactions of the Royal Society*, B350, 153-161.

RANSOME, R.D. 1996. The management of feeding areas for greater horseshoe bats. *English Nature Research Reports,* No. 174, 1-74.

RANSOME, R.D. 1997a. The management of greater horseshoe bat feeding areas to enhance population levels. *English Nature Research Reports,* No. 241: 1-62.

RANSOME, R.D. 1997b. Climatic effects upon foraging success and population changes of female greater horseshoe bats. *In*: B. Ohlendorf, ed. *Proceedings of the Nebra Rhinolophid Bat Conference 1995,* 129-132. Berlin: IF-A Verlages.

RANSOME, R.D. 1998. The impact of maternity roost conditions on populations of greater horseshoe bats. *English Nature Research Reports,* No. 292, 1-79.

RANSOME, R.D. 2000. Monitoring diets and population changes of greater horseshoe bats in Gloucestershire and Somerset. *English Nature Research Reports,* No. 341, 1-55.

RANSOME, R.D. 2002. Winter feeding studies on greater horseshoe bats. *English Nature Research Reports,* No. 449, 1-47.

RANSOME, R.D., & MCOWAT, T.P. 1994. Birth timing and population changes in greater horseshoe bat colonies are synchronised by climatic temperature. *Zoological Journal of the Linnean Society*, 112, 337-351.

SPEAKMAN, J.R., & RACEY, P.A. 1987. The energetics of pregnancy and lactation in the brown long-eared bat *Plecotus auritus* *In*: M.B. FENTON, P.A. RACEY & J.M.V. RAYNER, eds. *Recent advances in the study of bats 1987*. 367-420. Cambridge: Cambridge University Press.

WHITAKER, J.O. 1988. Food habits of insectivorous bats. *In*: T.H.KUNZ, ed. *Ecological and behavioural methods for the study of bats,* 171-179. Washington: Smithsonian Institution Press.

WHITE, E. 1960. The natural history of some species of *Aphodius* (Col. Scarabaeidae) in the northern Penines. *Entomologists Monthly Magazine,* 66, 25-30.

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